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METAMORPHIC AND IGNEOUS ROCKS OF EASTERN ECUADOR [1]

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I. INTRODUCTION

The rocks, from Eastern Ecuador, described in the following pages were collected during two exceedingly difficult journeys, one in 1921 (5) [2] and the other in 1927-1928 (4), in that part of eastern Ecuador called the "Oriente", lying between the Equator and 2° S. Latitude, and extending from the culminating peaks of the Andes Mountains as far east as the confluence of the Napo and Coca Rivers, 77° west of Greenwich.

The geological results of the first expedition were published in part as a memoir (7) which was limited almost entirely to a description of the sedimentary rocks and their fossils, the latter proving the presence in eastern Ecuador of sediments as old as the Albian subdivision of the Cretaceous period.

Considerable petrographic work has been done on rocks from the Andes of Ecuador, but practically none on those from the "Oriente" or forested foothills and lowlands east of the Andes. The volcanic mountains of the

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[2] Throughout the present paper italicized numbers enclosed in parentheses refer to references similarly designated in the bibliography.

lofty Andes, such as Chimborazo, Cotopaxi, etc., have been a favorite field of study for European geologists and the results of their investigations are set forth in so many papers that we cannot attempt to cite them all.

The German geologists, Wilhelm Reiss and Alphons Stubel, (3) may be singled out for mention because of their labors, extending over a period of five years, during which all parts of the Andes of Ecuador were visited. They made collections of the different rocks encountered and submitted them to German petrographers for study. In the course of their investigations they collected material from three localities on the western boundary of the area we are describing.

Reiss and Stubel worked in Ecuador from 1870 to 1874; in this period they collected about 6,000 specimens of igneous rocks. For the petrographic studies of these rocks over 1800 thin sections were examined by various petrographers. Even the bibliography pertaining to the work of Reiss and Stubel and their collaborators is too lengthy to be cited in this memoir.

Previous to the 1921 expedition of Sinclair and Wasson no pre-Tertiary fossils had ever been found in Ecuador. It was concluded, merely on the basis of similar rocks elsewhere, that the few outcrops of sedimentary rocks found here and there, in very disturbed conditions in the midst of igneous rocks, were of Cretaceous age. The igneous rocks of the Andean highlands of Ecuador have, however, been described as Tertiary and Quaternary lavas, and the metamorphic rocks, consisting of schists and gneisses, are thought by all geologists who have made field studies of them, to be very ancient.

The best description of the igneous rocks nearest our area is that of Von Wolff, (2) who gives in great detail the results of his petrographic examination of the Reiss and Stubel collection from the peaks of the Andes along the western border of our area.

The value of our collections from eastern Ecuador lies not only in the number of specimens and variety of igneous rocks represented, but in the fact that in this area, for the first time, the field relations between sediments of proven age, and a large series of altered volcanic rocks, were clearly seen. In the "Oriente" the Cretaceous sediments occur over wide areas in a nearly horizontal attitude and at times their lower beds may be seen underlain by certain of the igneous rocks. In the Andes it is impossible to tell whether the igneous rocks lie above or below the few sediments exposed.

The expeditions of 1921 and 1927 proved that volcanoes, hitherto thought to be limited to the high Andes, are likewise present in the foot-

hills and lowlands far to the east. The great volcano "Sumaco" lifts its mighty cone in the midst of the Cretaceous rocks of the foothills. In 1926 a new and hitherto unknown volcano, called by the Indians "El Reventador", came into activity at a point about 30 miles east of the main Andes, and it is possible that other volcanic centers may be discovered later.

With the exception of several specimens of recent lavas collected from lava streams which have flowed down the slopes of Antisana to the Oriente, and from other localities which may represent isolated outflows of lavas, no other specimens of *recent* lavas were collected by the expeditions of 1921 and 1927, because these are so widely distributed in the Andes immediately to the west and because they have been previously described.

The only specimens of recent lavas from *eastern* Ecuador previously described in geological literature (*1*) proved to be unique in that they are the first feldspathoid lavas so far known in all of Ecuador.

II. PHYSIOGRAPHIC FEATURES

The region from which the collections were made is intermediate between the lofty summits of the Andes and the low-lying Amazon plain. On the west are the great snow and glacier-capped peaks of Cayambe (19,000 feet), Antisana (18,700 feet), Cotopaxi (19,300 feet), Tungurahua (16,500 feet), El Altar (17,400 feet) and Sangay (17,100 feet). On the east, at the confluence of the Napo and Coca Rivers, and only ninety miles from the above line of summits, elevations as low as 850 feet above the sea are found. This general slope is interrupted by minor mountain masses, themselves of great elevation and prominence. The gigantic volcanic cone of Sumaco, for example, rears itself to an elevation of 12,500 feet half-way between Antisana and the confluence of the Napo and Coca Rivers. The still unexplored Galeras Mountains, twenty-eight miles south of Sumaco, have summits about 5,400 feet above sea level and the volcano "El Reventador", recently become active and situated about forty-five miles north of Sumaco, is a prominent mass about 6,000 feet above sea level. Thus, the area is one of strong topographic features.

The rivers descend from the snow-covered summits of the Equator in profound gorges, leaping in places down great cataracts and reaching the "fall line", in almost continuous rapids, at about 850 feet elevation.

III. DIFFICULTIES OF EXPLORATION

The difficulties of exploring this region are made almost insurmountable by the excessive rainfall which, in places, attains seventeen feet per an-

num, and by forests which cover the entire area up to an elevation of about 10,000 feet above the sea. In these forests the few footpaths are but gloomy tunnels through the vegetation, where the traveller wallows knee-deep in mud and is subjected to a constant downpour from rain and from the dripping trees. The temperature and climatic conditions vary from the tropical heat prevalent at the mouth of the Coca to the snow storms of the high passes, which have an elevation of 13,000 feet. The population is exceedingly limited. Dwellings of Indians are found at very rare intervals and the occasional widely separated villages of the white pioneers have very few inhabitants.

IV. PETROGRAPHY

The forty-four samples of rocks described in the following pages, collected east of the Andes during the two expeditions of 1921 and 1927, may be divided into five groups:

A. Metamorphic rocks; schists of various types.

B. Igneous rocks; chiefly surface types, of proven pre-Albian age.

C. Igneous rocks; chiefly surface types, probably also pre-Albian, but whose age is not certain because their outcrops are distant from occurrences of sediments of known geologic horizon.

D. Granites.

E. Lavas of late Tertiary, Quaternary and Recent age.

The name of each rock and the group to which it belongs on the basis of the above classification are shown in Table I.

The igneous rocks, excepting the granites and schists, might be subdivided into two sub-groups, (1) surface flows and tuffs, of unquestioned pre-Tertiary age because of the profoundly altered condition of the rocks; and (2) volcanic rocks of Tertiary to Recent age, because of the lack of alteration of any of the primary minerals.

A. METAMORPHIC ROCKS

THE SCHISTS

The "core" of the Andes of Ecuador consists of metamorphic rocks, schists and gneisses, of unknown age, although they are generally considered pre-Paleozoic and are judged to be a part of the wide-spread formation of the same character common in many parts of South America.

TABLE I.

		Locality	Sample No.	Name of Rock
METAMORPHIC	SCHISTS	Río Papallacta	1	Orthoschist of complex origin
		Río Papallacta	2a	Orthoschist of complex origin
		Río Papallacta	1a	Quartz sericite schist
		Río Papallacta	3	Sheared rock; mylonitized
		Río Papallacta	4	Helicitic mica schist
		Río Papallacta	5	Sismondite schist
		Río Papallacta	5a	Sheared meta-diorite porphyry
		Río Papallacta	6	Sheared meta-diorite porphyry
		Río Papallacta	6a	Sheared meta-diorite porphyry
		Río Papallacta	7	Orthoschist (Greenstone schist)
		Río Quijos	8	Biotitic schist of complex origin
		Río Quijos	9	Schistose rock of complex origin
IGNEOUS	(a) PRE-ALBIAN (PRE-MIDDLE CRETACEOUS) VOLCANICS	Río Coca	1L	Devitrified acid volcanic tuff
		Río Coca	L-a	Devitrified volcanic ash
		Río Coca	Z	Meta-andesite
		Río Coca	1	Trachy-andesite or latite
		Río Coca	1-a	Latite tuff or tuffaceous latite
		Río Coca	2	Acid volcanic tuff
		Río Coca	3	Spherulitic felsite
		Río Coca	4	Volcanic tuff
		Río Coca	5	Modified basalt
		Río Coca	6	Andesitic tuff
		Río Coca	17	Basaltic andesite
		Río Coca	18	Porphyritic latite
		Río Misahualli	A	Tuffaceous trachytic felsophyre or modified trachytic ash.
		Río Misahualli	69	Trachytic felsophyre
		Río Misahualli	71	Altered basaltic amygdaloid
		Río Misahualli	72	Altered basalt
		Río Misahualli	72-C	Altered amygdaloidal basalt
		Río Misahualli	73	Dellenitic tuff
		Río Jandache	B	Dellenitic vitrophyre
	(b) PROBABLE PRE-ALBIAN VOLCANICS. Excepting Nos. 11 and 12.	Río Pastaza	7a	Rhyolite
		Río Pastaza	7c	Rhyolite
		Guacamayos Mt.	A	Weathered monzonite porphyry
		Guacamayos Mt.	B	Spherulitic granophyre
		Guacamayos Mt.	C	Gabbro, much altered
		Río Papallacta	2b	Silicified, kaolinized andesite Included here for convenience.
		Río Quijos	12	Serpentinized rock
		Río Quijos	11	Limestone breccia
	(c) GRANITES	Río Urcusikiyacu	a	Biotite granite
		Río Napo	b	Biotite granite
		Río Pastaza	7b	Graphic granite
	(d) QUATERNARY LAVAS	Río Papallacta	10	Basalt
		Río Cosanga	2	Andesite

In Ecuador these schists and gneisses outcrop from the Peruvian to the Colombian borders in an almost continuous, narrow band, running nearly north and south like the main Andean cordillera. The line of lofty volcanic peaks forming the eastern boundary of the high Andes and the eastern slopes of these mountains down to what may be called the base of the Andes are included in this area.

The schists are exposed at elevations as high as 13,448 feet [3] above the sea in this belt in Ecuador. In the western part of the Andes they are generally concealed beneath enormous masses of lavas and tuffs, the products

[3] Feldspar-rich mica schists, somewhat phyllitic, from the west summit of Jacatuna de Numuloma western foothills of Antisana, according to Reiss and Stubel.

of Tertiary and recent volcanic action. It is fairly logical to conclude that these schist are the oldest rocks of Ecuador. The peculiar narrowness of their outcrop suggests that they form the exposed base and sides of a great fault-block which is tilted westward toward the Pacific Ocean.

The schists described in this memoir were collected from the Papallacta gorge, one of the great gorges which cut into the eastern slope of the Andes, in which waters of the Río Papallacta and the Río Quijos unite to form the Río Coca. They were first encountered at an elevation of 9,100 feet; proceeding eastward down the gorge they disappear at an elevation of 6,100 feet. They thus outcrop in a vertical range of 3,000 feet. The width of this belt in the Papallacta gorge is about fourteen miles. At the upper boundary in the vicinity of the village of Papallacta they vanish beneath late Tertiary lavas and tuffs and do not reappear anywhere in the thirty-three miles between this point and Quito, although during the traverse we ascended to over 13,000 feet above the sea and descended as low as 7,100 feet.

The nine samples collected in the above named gorge are intensely metamorphosed rocks. They are all crystalline schists, folded, crumpled, and presenting all the aspects of rock that has been subjected to regional dynamic metamorphism in conjunction with attack from a subjacent igneous source. They present an exceedingly complex history involving an origin that in some cases was certainly igneous, in others probably sedimentary.

Since there are some interesting features connected with the samples they are here described in detail. Furthermore, with the exception of the three samples collected by Reiss and Stubel in August 1871,[4] no description has been published of these Papallacta Valley schists.

Specimen No. 1 was collected from a massive outcrop 2.5 miles east of the hamlet of Papallacta, on the left bank of the river along the trail at an elevation of 9,404 feet.

It is a light gray rock with variable texture, carrying much glistening scaly sericite; it is very streaked and heterogeneous in make-up, coarse, foliated and strongly sheared, with the general aspect of a schist.

Petrographically the rock proves to have been initially igneous in origin: either a granite or granodiorite. The original character is considerably obscured by shearing and by reason of the changes brought about through the modification of the former components by the attack

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[4] The collection of Reiss and Stubel consists of a "phyllite gneiss" from the church at the village of Papallacta, boulders of phyllite gneiss in the Río Papallacta at the mouth of the Yurac-yacu and a "muscovite mica schist" carrying abundant carbonaceous matter from the Papallacta valley between the hamlet of Papallacta and the mouth of Yurac-yacu.

of igneous matters. There is, therefore, an antecedent structure within the rock, inherited from a former condition, and in addition secondary structures imposed upon it as well. The original minerals consisted largely of hypidiomorphic plagioclase feldspars, biotite, and perhaps quartz, although it is uncertain how much of the quartz was present initially as primary orthotectic quartz and how much invaded the rock during the later metamorphic stage.

The plagioclase is fractured and microfaulted; the older plagioclase is almost wholly, if not entirely, replaced and modified so that only the "ghosts" of it remain. The modification products consist of little prisms of zoisite, grains of epidote, shreds of sericite, little grains of garnet, some of them quite idiomorphic, and turbid patches composed of a very minutely granular aggregates of the same set of products just mentioned, that correspond to saussurite. All of these products are confined within the limits of what was the original plagioclase; they are now included in new crystals of albite that extend beyond the limits of the older plagioclase and which have largely replaced the older feldspar. In places the albitized plagioclase has taken on a "pseudo-perthitic" structure due to deformation, subsequent to the period of replacement, that ruptured and displaced the albite twinning so that the feldspar, at first glance, resembles microperthite. Only the merest traces of the structure and the substance of the earlier plagioclase are preserved, but the *forms* of the older plagioclase are in places emphasized by the groups of alteration products just referred to.

The biotite seldom retains any semblance of its original form; it is commonly squeezed out into streaks composed of fine shreds and minute flakes of colorless mica mixed with yellowish-white opaque specks of leucoxene, specks of iron-oxide and grains of quartz. There are a few remnants that still retain some suggestion of their original shapes, but even these are bent and distorted, and all of them are altered in the manner described.

The later albite is filled with both crystal and bubble and liquid inclusions, roughly oriented, and commonly intersecting the cleavage directions at an oblique angle.

Quartz, albite and a little muscovite were introduced into the rock during the later stages of its metamorphism, transecting fractured feldspars and distributed in streaks and patches. Even the later quartz and albite that were introduced and whose feldspar has in part replaced the older feldspar of the rock, have been deformed by fracturing and granulation, so that at least two stages of deformation are recorded; one was

connected with the period of "soaking" by granitic juices that effected re-placement of earlier feldspars and the "granitization" of the rock; the other, and later, post-granitization period of deformation granulated and fractured both the granitized rock and the replacement matter. In addi-

FIG 1 —*Papallacta No 1*—Orthoschist of complex origin   Drawing, ordinary light, showing relics of older feldspar in later albite   The older feldspar consists of aggregates of zoisite-epidote-sericite, garnet grains, and minutely granular aggregates of the same set of products   Colorless areas are quartz with inclusion trains   × 13

tion, there is evidence that the introduction of quartz continued subse-quent to the later deformation, since in both No. 1 and No. 2a there are areas of quartz and associated calcite in granular mosaic aggregates that exhibit no signs of deformation at all.

Specimen No. 2a, taken 6.7 miles east of Papallacta at an elevation of 8,571 feet, is similar to No. 1 in character, structure and history. This is a light colored, streaked and schistose, coarse textured rock. The plagio-

clase is fractured and crowded with innumerable inclusions consisting largely of coarse sericite, with less epidote and zoisite, garnet grains, granular titanite and chlorite. The same set of products mixed with granular quartz, albite and a little pyrrhotite, are distributed along fracture zones as well. There is considerably more calcite associated with the introduced quartz and feldspar than in Specimen No. 1, but the two specimens are very much alike in other respects.
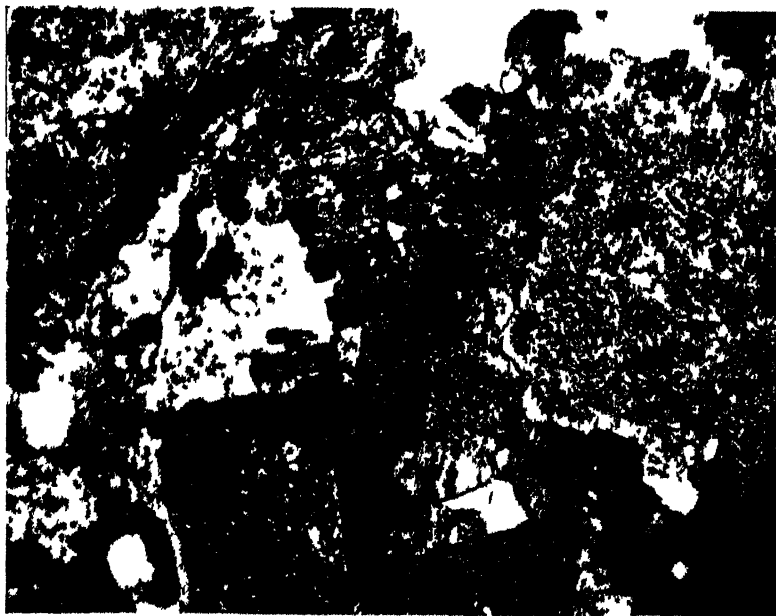
Fig. 2   Papallacta No 1   Photomicrograph of the same schist shown in Figure 1, nicols crossed   Note the relic structures of older feldspar in later albite, and the granular aggregate of zoisite epidote sericite in the fresh albite   ×34.

Despite the fact that these two specimens were secured from exposures four miles apart and differing in elevation eight hundred feet, they are essentially alike in composition, and the sequence of events recorded in them is the same.

Some of the features described are shown in Figure 1, which is a drawing from a thin section of Specimen No. 1, and in Figure 2, a photomicrograph of Specimen No. 1, taken with nicols crossed.   The drawing, which represents the appearance of the section in ordinary light, shows the older plagioclase crowded with very fine, dense aggregates of epidote-

zoisite, mixed with larger grains and prisms of the same minerals, in an albite matrix that extends in clear areas beyond the original margins of the older plagioclase.

The photomicrograph (Fig. 2), taken at a lower magnification than the drawing (Fig. 1), illustrates the same set of conditions. Although there is little suggestion of schistosity in either the drawing or in the photomicrograph, the rock itself is not only coarsely foliated but exhibits injection effects as well. It is clearly an orthoschist, but it has an added complexity due to soaking, injection and resultant modification and replacement brought about either by an attack of the end-stage concentration-residua of the same magma that gave birth to the granodiorite or to an attack by a later magma.

TABLE OF ANALYSES

		1	2	3	4	5	6	7	8	9
Silica	SiO_2	67 54	67 18	59 47	66 10	65 30	60 42	60 50	56 76	63 40
Alumina	Al_2O_3	15 26	15 45	16 52	15 32	13 02	16 32	18 20	16 20	16 57
Ferric Oxide	Fe_2O_3	1 29	1 75	2 63	1 97	1 17	1 93	4 52	4 16	1 90
Ferrous Oxide	FeO	2 82	2 27	4 11	2 90	4 71	2 62	0 86	3 36	1 90
Magnesia	MgO	2 85	1 55	3 75	1 77	2 87	3 82	2 87	4 04	2 14
Lime	CaO	2 16	3 57	6 24	3 81	0 98	5 06	2 39	5 82	3 83
Soda	Na_2O	4 94	3 63	2 98	3 48	1 12	4 41	4 63	3 93	4 77
Potassa	K_2O	0 92	2 79	1 93	2 74	2 47	0 65	1 90	2 39	3 48
Water 110°	$H_2O -$	0 04		1 39	1 06	0 00	0 01	0 59		
Water over 110°	$H_2O +$	0 81				1 93	0 90	1 96		
Titanium Oxide	TiO_2	0 68	0 50	0 64	0 53	0 50	0 58	0 74	0 96	0 18
Phos Pentoxide	P_2O_5	0 10	0 23	0 26	0 27	0 10	0 10	0 10	0 25	0 21
Manganous oxide	MnO	0 28	0 21	0 08	0 04	0 39	0 47	0 50	0 12	0 07
Sulphur tri-oxide	SO_3	0 07				0 03	0 09	0 09		
Carbon dioxide	CO_2	0 01				0 29	1 72	0 04		
	Iron (as Fe)						0 37			
	S (as S)						0 21			
TOTAL . .		99 80				99 85	99 68	100 18		

1. Sample No 1 Papallacta. Analysis by Ledoux & Co, New York
2. Average of 10 analyses of granodiorites
3 Average of 20 analyses of quartz diorites Daly, R A, Igneous Rocks and Their Origin, 1914, p. 26
4. Average of 37 analyses of tonalite, quartz monzonite, granodiorite Daly, R A, Idem, p 25.
5. Sample No 5, Papallacta Analysis by Ledoux & Co, New York
6. Sample No 6, Papallacta Analysis by Ledoux & Co, New York Note This sample contains pyrite and traces of galena
7. Sample No 6, Río Coca Analysis by Ledoux & Co, New York
8 Average of 12 analyses of andesites Bul 419, U S G S, 1910
9. Average of 6 analyses of diorite porphyry Bul. 419, U S G S, 1910

Comment on Analysis: An analysis of the rock, compared with averaged analyses of 10 granodiorites, 20 quartz diorites, and a combined average of 37 analyses of tonalite, quartz monzonite and granodiorite, shows marked differences in the proportions of certain of the constituents, more especially when the analysis of Papallacta No. 1 is compared with the average for granodiorite.

The average granodiorites (Nos. 2 and 4, table of analyses) carry three times as much potash as sample No. 1 from the Papallacta trail, but only two-thirds as much soda. The lime is higher in the average granodiorites, but the magnesia is considerably lower. The percentages of silica and alumina, however, in the averaged analyses of granodiorites, are nearly equal to the silica and alumina in sample No. 1, Papallacta. The analysis of the Papallacta rock is not at all comparable with the average of twenty analyses of quartz diorites, which is included here merely for the purpose of extending the range of comparison. These differences in the composition of the Papallacta rock, compared with the composition of average granodiorite, may be due in part to the entrance of igneous emanations from a subjacent source, and the replacement of feldspar, originally richer in potash, by soda-rich emanations. While the rock, judging merely from the thin section, is a sheared and modified granodiorite, it is probable that this particular specimen happened to contain more of the granodiorite material than of the older schist invaded by the granodiorite, so that there are but traces of the older schist in this sample.

Specimen No. 1-a, 2.5 miles east of Papallacta, elevation 9,404 feet, is a moderately fine textured *quartz-sericite schist* of uncertain initial origin. Although the sample was secured in the same place as No. 1, there is but little resemblance between them except in the matter of certain minerals that are common to both. The rock consists of quartz, prisms of zoisite and epidote, streaks and plates of chlorite and muscovite, a little blue-green amphibole, clear untwinned feldspar of lower index than balsam ($< 1.535 +-$) and with extinction angles measured from cleavages that range from $10°$ to $30°$, a most unusual feature; granular titanite, crystals of zircon and a little pyrrhotite, all oriented in the plane of schistosity of the rock. The streaks and plates of muscovite and chlorite, the little prisms of epidote, zoisite and blue-green amphibole and some of the quartz that is elongated in the plane of schistosity, are responsible for the schistose structure. But there are streaks of quartz and feldspar that are quite granular and mosaic-like and which impart no schistosity to the rock at all. These have the character of injected matter derived

from an igneous source; that is, these streaks are judged to be *lit-par-lit* injections of a sort.

There is no direct evidence bearing on the initial condition of the rock; it is impossible to determine whether it represents an intensely metamorphosed sediment or whether it is a strongly sheared and highly metamorphosed portion of the granodiorite, although it seems more probable that this sample represents the older schist, of sedimentary origin, rather
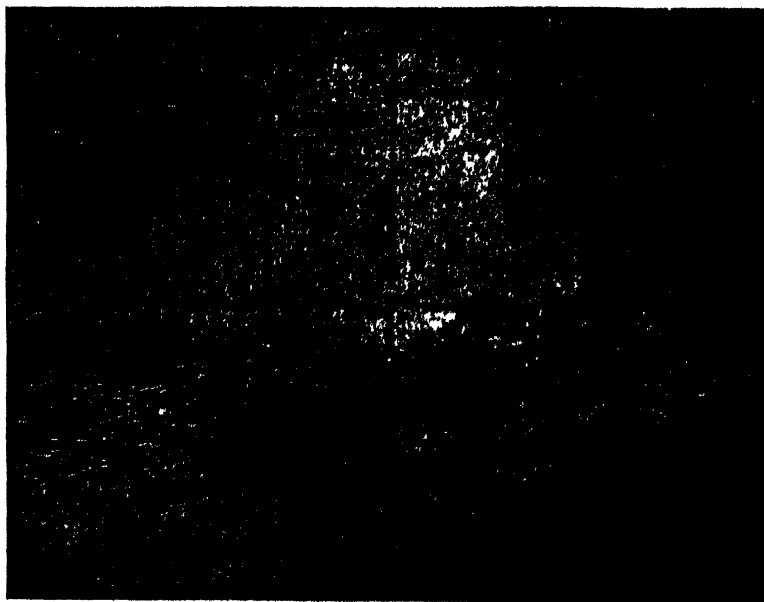
FIG. 3 *Papallacta 1a.*- Quartz sericite schist Photomicrograph, ordinary light, showing schistosity. The band in the upper half of the picture is a granular mosaic of aggregate quartz with undeformed grains. The large darker gray patches are chlorite, the small grains and prisms are epidote and zoisite, the lighter colored foils and needles are sericite. ×24.

than an intensely sheared phase of a massive rock like the granodiorite. Whatever the original condition, the rock has not only been converted into a crystalline schist, but it has also been affected by injections of matter under igneous control, a circumstance favoring the conclusion that this specimen represents some of the older schist of probable initial sedimentary origin.

The character of this rock is shown in Figure 3, which illustrates some of the conditions described and which presents a striking contrast to

Specimen No. 1, Figures 1 and 2, although both samples came from the same locality.

Specimen No. 3, 7.5 miles east of Papallacta, elevation 8,330 feet, is a coarse textured, brown, iron-stained, chalky-spotted, sheared rock resembling a sheared and weathered granite or granodiorite. It has been subjected to crushing of considerable intensity, so that the rock is more or less mylonitized, and much limonitic matter has developed, together with a white, opaque substance distributed in streaks that cut all the other minerals in the rock. There are uncrushed patches and streaks of coarsely granular, interlocking mosaic-aggregates of quartz, areas composed of very fine, brilliantly polarizing, flaky aggregates of colorless mica, and coarser muscovite, in aggregate groups, that is associated with alkali feldspar and that carries innumerable inclusions oriented transverse to the cleavage of the mica; under high magnification these prove to be long and narrow cavities filled with liquid and bubbles.

There is evidence indicating two stages of deformation; the earlier was the more intense. It is judged that during this stage the rock was crushed and granulated. The other and later period was productive of fractures that cut all of the other structures in the rock. Surface agencies have attacked the rock along these later weaknesses with the production of limonitic matters.

While the initial character of the rock is very obscure, it is probably an extensively sheared phase of the granodiorite.

Specimen No. 4, 9 miles east of Papallacta, elevation 8,114 feet, is strongly schistose, folded and crumpled, black and white laminated, and very micaceous. It has all the aspects of a soaked, injected, silvery mica schist.

In thin section it exhibits an extremely striking helicitic structure, by reason of the replacement of the body of the schist with granular quartz and an optically positive feldspar that is occasionally twinned after the Carlsbad law, whose indices of refraction are lower than the index of the balsam, and with extinction angles as high as 25° measured from well developed cleavage; a feature similar to that mentioned as occurring in Specimen No. 1a.

The crystals of feldspar are allotriomorphic to hypidiomorphic, very rarely exhibiting albite twinning. They are metapoikilitic, carrying many inclusions consisting of minute blebs of quartz, many small prisms of zoisite, grains of zircon, little tourmaline crystals, epidote grains, titanite grains, prisms of apatite, and considerable fine, black and possibly carbonaceous or graphitic matter, all distributed in a crumpled, schistose

structure that passes indifferently through the grains and the boundaries of the grains of the replacing quartz and feldspar, as well as through crystals of muscovite that is associated with the quartz and feldspar. These "ghosts" of schistosity serve to emphasize the relic structure in the schist.

There are also bands of clear aggregate quartz, likewise mixed with feldspar and with a very faintly green, beautifully twinned clinochlore.

The specimen shows more or less clearly:

FIG. 4.—*Papallacta No. 4.* Helicitic mica schist. Drawing, ordinary light, showing helicitic structure. The relic schist structure, now preserved in the form of carbonaceous dots and streaks, passes through the later replacing quartz and feldspar, which of itself is not schistose at all. ×24.2.

(*a*) The development of a schist from an unknown, but probably sedimentary, original, by metamorphic processes of considerable intensity. The schist may have been initially a phyllite derived from a sediment, somewhat crumpled, and perhaps somewhat graphitic.

(b) Soaking, injection and actual replacement by end-stage concentration residua from a granitic or granodioritic source; much of the quartz and all of the feldspar belong to this stage, and it is probable that the clinochlore and muscovite are products formed by the action of the emanation-residua on the matter composing the original schist.

This very striking rock, with its beautiful helicitic structure and clearly indicated history of the replacement of an original phyllite by emanations from a magmatic source, is illustrated by Figure 4, drawing
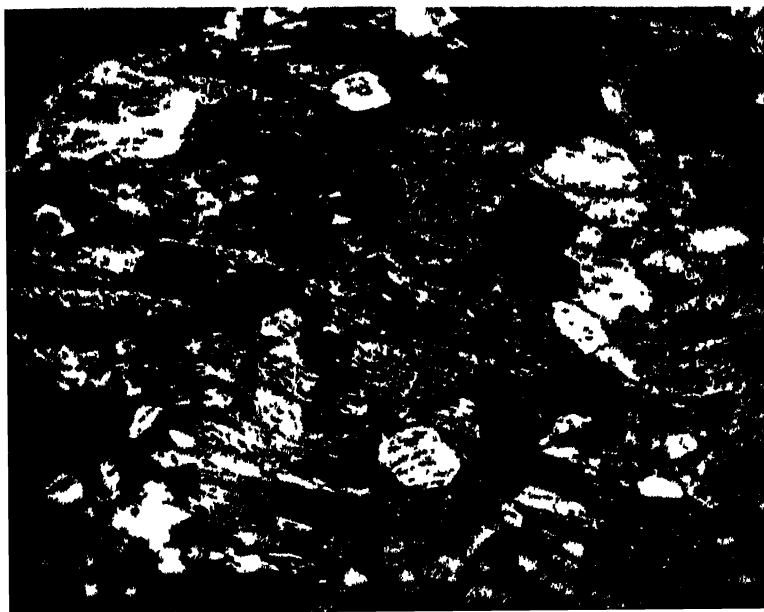
FIG. 5   Papallacta No. 5. Photomicrograph of the same schist shown in Figure 4, nicols crossed. Note the granular aggregates of undeformed quartz and albite, replacing the substance of the rock, and containing ghost structures of the original phyllite.   ×24.

made in ordinary light, showing the relic structure of the schist passing indifferently through the replacement-mosaic of quartz and feldspar; and by Figure 5, a photomicrograph taken at a lower magnification than that represented by the drawing, showing the aspect of the section between crossed nicols.

Specimen No. 5, 10.1 miles east of Papallacta, elevation 7,579 feet, is a fine textured, silvery gray, *muscovitic schist,* composed of quartz elongated in the plane of schistosity, long sinuous streaks of muscovite

that at times enclose microscopic augen composed of compound grains of quartz; and prisms, bundles, groups and rosettes of a colorless variety of chloritoid corresponding to sismondite. The rosettes are formed of prismoids radiating from centers that consist of unit and compound quartz grains filled with minute included grains of sismondite. The

Fig. 6. *Papallacta No. 5.* Sismondite schist. Drawing, ordinary light, showing rosettes, grains and prismoids of ottrelite (sismondite). The colorless portions are quartz. Schistosity due to arrangements of sismondite also shown. × 13

prisms exhibit polysynthetic twinning, a common characteristic of ottrelite; the lack of both color and pleochroism suggests, however, that the crystals carry more magnesia and much less iron than ordinary ottrelite. The analysis of the rock supports this statement; most of the magnesia reported in the analysis is probably contained in the sismondite, since the only other essential components in the rock are muscovite and quartz. There are minutely microscopic crystals of rutile sparsely disseminated

in the rock, many exhibiting geniculate twinning on a microscopic scale. Provided the greater part of the magnesia is contained in the sismondite, the rock should carry almost 15% of that component. This corresponds approximately with the mineral composition exhibited by the section.

Comment on Analysis: The alumina (18.02%) is higher in proportion to the silica (65.30%) than is normal for a rock carrying the amount of combined alkalies ($K_2O + Na_2O = 3.59\%$) that this one does, and
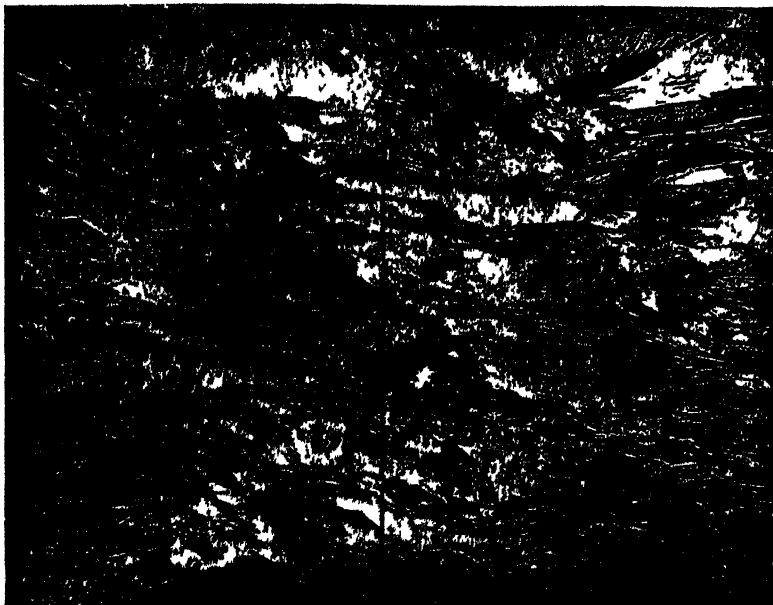
Fig. 7. *Papallacta No. 5.* Photomicrograph of the same schist shown in Figure 6, ordinary light. Rough, high relief prisms and grains are sismondite. The lower relief streaks are muscovite, the plain, smooth areas are quartz   ×33.

the lime (0.98%) is relatively low (see Table of Analysis), assuming the schist to have been derived from an igneous rock. The potash and soda are probably contained for the most part in the muscovite, although some of the soda may be in the sismondite. The iron is probably distributed in large part in both the muscovite and sismondite.

From the chemical composition and mineralogical make-up of the rock, it is judged that this quartz-muscovite-sismondite schist was derived by intense dynamic metamorphism from a former sediment, rather than from an igneous rock.

The character of the rock is illustrated by Figure 6, drawn from the thin section in ordinary light, and by Figure 7, a photomicrograph taken in ordinary light. Some of the prismoids and rosettes of sismondite, the muscovite and quartz, and the general schistose habit of the rock, are shown.

Specimens Nos. 5a, 6, and 6a are much alike. No. 5a was secured in the same locality as the sismondite schist No. 5, just described, 10 miles east of Papallacta. Nos. 6 and 6a came from a locality 10.7 miles east of Papallacta, at an elevation of 7,561 feet.

All of these rocks are intensely sheared and thoroughly metamorphosed porphyries that were probably initially dioritic in composition. In No. 5a the original phenocrysts of plagioclase feldspars now consist of finely granular aggregates of zoisite, epidote and albite, a little calcite and occasionally a little quartz and chlorite. Much finely granular epidote is also distributed through the groundmass, which has been entirely recrystallized into a crudely oriented, interlocking, crystalline aggregate of granular quartz, albite, garnet grains, calcite, and shreds, streaks, patches and corroded crystals of biotite. Many of the albitized phenocrysts show partial replacement by epidote and zoisite and more or less granulation along their margins; in a few instances they have been subjected to much more extensive granulation. These rocks are intensely sheared, epidotized, albitized (saussuritized), modified and reorganized metadiorite porphyries.

The groundmass of Samples No. 6 and 6a is a recrystallization and modification complex of quartz, albite, epidote, calcite, muscovite, clinochlore, and a little pyrite and pyrrhotite.

The saussurite pseudomorphs after the plagioclase phenocrysts act as augen of a sort, since the groundmass minerals swing around them in lines of dynamic flowage. In Nos. 6 and 6a the same set of conditions prevails but most of the original feldspar phenocrysts are albitized and not so thoroughly saussuritized as those in Specimen No. 5a. Others have been partly, and some wholly, converted into coarsely crystalline aggregates of epidote. Corroded brown hornblende crystals are sparingly distributed in the groundmass, as well as ragged patches and streaks of clinochlore.

Some of the features mentioned are shown in Figure 8, a photomicrograph of Sample No. 5a, taken in ordinary light. The black patches are minutely granular saussuritic aggregates pseudomorphous after original plagioclase phenocrysts. The completely recrystallized and modified groundmass consists largely of quartz, albite, and biotite. The innumer-

able minute dots in the quartz and albite of the groundmass are bubble and liquid inclusions.

Comment on Analysis: An analysis of Sample No. 6 is given in the table of analyses, and for comparison the average of six analyses of diorite porphyry is likewise included.

The silica in Papallacta No. 6 is lower than the average of the diorite porphyries, but all the other constituents with the exception of potash
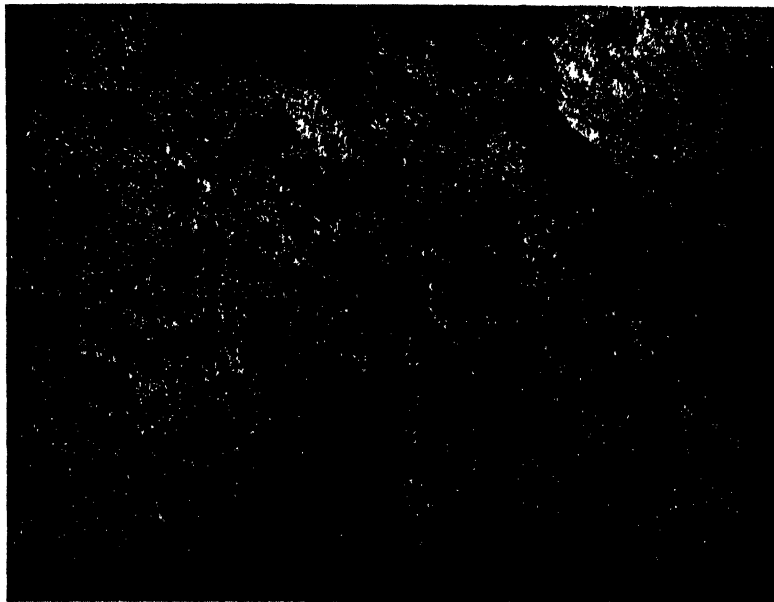
FIG. 8. *Papallacta No. 5a.* Sheared and modified metadiorite porphyry. Photomicrograph, ordinary light. The black crystals are pseudomorphs of finely granular saussurite (extremely finely granular aggregates of zoisite-epidote-albite) after feldspar phenocrysts. The groundmass is composed of granular quartz and feldspar and little biotite crystals which are filled with minute bubble inclusions.   ×24.

and manganous oxide are in reasonable agreement, although both magnesia and lime are higher in the Papallacta rock. There is less than one-fifth as much potash and almost seven times as much manganous oxide in Papallacta No. 6 as shown by the averaged analyses of diorite porphyry. Among the superior analyses of igneous rocks listed by Washington (6), in only two of twenty-three analyses of diorite porphyry cited is the potash less than one per cent., and in but one analysis is less than three per cent. of soda reported.

The average potash content of the twenty-three analyses is 2.52%, the average soda content 4.14%, figures comparable with the averaged alkali content of the six diorite porphyries listed in the table of analyses.

Excepting the low potash content, the composition of Sample No. 6 Papallacta is comparable with the compositions of diorite porphyries the world over, so that the shearing and metamorphism of the rock may have resulted in the development of schistosity and in recrystallization of the primary substances without the addition of any other constituent and without the subtraction of any material from the rock, unless some of the potash originally present was eliminated during metamorphism, and a little soda, and perhaps water, added.

Sample No. 7, 12.5 miles east of Papallacta, elevation 6,972 feet, is quite different from the preceding specimens. It is a fine, schistose, indurated green rock. The color of the rock is due to abundant, emerald green, strongly pleochroic plates of lamellar clinochlore, oriented in the plane of schistosity. Both epidote and zoisite in grains, prisms and aggregate masses are likewise abundant, and the rock contains much granular quartz and alkali feldspar, some in the form of albite, some as allotriomorphic, untwinned grains. Quartz, feldspar, clinochlore, epidote and zoisite make up nearly the whole of the rock. There is a little colorless mica occasionally intergrown with the clinochlore, and there are bands of mosaic quartz, parallel to the schistose structure of the rock, that have the aspect of later, or injection, quartz. The initial character of the rock is very obscure, but the composition of it, as observed in thin section, suggests derivation from an igneous rock of medium basic character, perhaps somewhat similar to the sheared, albitized and metamorphosed diorite porphyries Nos. 5a, 6 and 6a, although the large amount of chlorite and epidote, and the lack of remnants of former phenocrysts, as well as the finer texture, suggest derivation from an igneous rock such as andesite or basalt. It is essentially a greenstone schist in its present condition.

Specimen No. 8, 11.1 miles east of Papallacta, elevation 6,600 feet, is a moderately fine textured, greenish-gray, strongly biotitic schistose rock. The schistose structure is caused by shearing and recrystallization. The biotite, but crudely oriented, is distributed in long streaks and in ragged scales, flakes and patches. It is light brownish-green in the position of maximum absorption, and almost colorless in the position of least absorption. Many of the biotite flakes carry included grains of epidote and an occasional one exhibits deep brown pleochroic haloes around minute included crystals of some sort, perhaps microscopic zircon crystals. There

is a little pale green clinochlore with characteristic polysynthetic twinning, and much almost-colorless epidote and associated zoisite, in swarms of grains, in larger prismatic crystals and in groups of grains. These are very prominent minerals in the rock. There is also considerable mosaic-like quartz and a pseudoperthite similar to that mentioned as present in Specimen No. 1, consisting of former plagioclase that was albitized and sufficiently deformed during subsequent shearing of the rock to have developed interrupted and offset albite twinning that resembles at first glance a microperthitic structure. Very much less prominent accessory minerals are muscovite, random small crystals of garnet, granular titanite, and a little pyrite in sharply euhedral and undeformed crystals.

Some of the quartz is distributed in mosaic-like grains that exhibit no crush-structures whatever, acting as hosts for assemblages of epidote-zoisite grains; but there are other places in the section where both quartz and feldspar have been granulated. While the original character of the rock is obscure, the composition and mineral assemblage suggest that it may have been derived from the same granodiorite that was the source of Specimen No. 1. It is a biotitic schist of uncertain origin.

Specimen No. 9, 16 miles east of Papallacta, elevation 6,375 feet, is a fine, streaked, silvery gray schistose rock. Local areas within the section are schistose, but there is no constancy of orientation of the grains. There are, however, shear structures of later origin that cut all the other structures in the rock, and along these weaknesses a little muscovite, prisms of zoisite, epidote, and considerable carbonate, pyrite and pyrrhotite are distributed. The sulphides must have been introduced, however, subsequent to the periods of deformation, since they cut and in part replace other minerals in the rock; they are distributed interstitially in irregular stringers, they cut through quartz, feldspar and carbonate indifferently, and they transect prisms of zoisite and epidote and fill the transverse fractures in them. The same situation prevails, in part at least, with respect to the magnetite. The calcite also encroaches on other mineral grains, although the sulphides, as previously stated, are distinctly later than it, according to the structural relations between the two minerals.

Quartz and albite are prominent minerals in the rock, both full of minute inclusions in the form of opaque (magnetite?) and transparent grains, and short, stout, but extremely minute crystals and long transparent "needles." The feldspar is albite, nearly all of which has suffered deformation; much of it exhibits interrupted and off-set twinning and

carries swarms and trains of liquid and bubble inclusions in addition to those already enumerated. Most of the "needles" resemble long, thin cavities rather than crystals. They are interrupted by cross fractures, they are irregular in width, they are teminated by rounded ends and many of them contain minute inclusions themselves which may, perhaps, be excessively small bubbles. The rock is probably a sheared portion of the granodiorite.

B. Igneous Rocks

A. PRE-ALBIAN VOLCANICS

In three localities in eastern Ecuador, on the Río Coca, the Río Misahualli and the Río Jandache, the sedimentary rocks which are only slightly inclined, are underlain by greatly altered volcanics, most of them modified tuffs. The remarkable similarity of these igneous rocks from widely separated localities, and their similar relation to the same sediments, lead us to believe that these igneous rocks are of the same age.

Fossiliferous limestones of Albian (Middle Cretaceous) age are separated from contact with these igneous rocks by only a few feet of sediments; in one place they are sandstones, in another, similar limestones. It is possible that among these beds beneath the Albian marine limestones are representatives of all or some of the Ordovician, Devonian, Carboniferous, Jurassic and Lower Cretaceous sediments that are found in Peru only a few miles to the south.

It is certain that these igneous rocks are of Pre-Albian age. It is probable that they are very much older, because they seem to be surface accumulations of lava and tuffs and not intruded igneous rocks, and were therefore deposited on a land surface which had to be depressed to permit the invasion of the sea and the accumulation of the Cretaceous marine deposits.

The thickness of these igneous rocks is unknown; we have not seen their base exposed. In each of the three localities where we studied them there was about 100 feet of them beneath the lowest beds of the sediments.

In the adjacent high Andes there are igneous rocks of similar composition and alteration which probably belong to the same formation. Below we shall discuss the probability that the felsites, andesites, porphyries, granophyres and gabbros of the Río Pastaza, Río Papallacta and the Guacamayos mountains belong to the same series.

Río Coca Series

The twelve samples from the Río Coca were collected from massive rocks outcropping in the banks of the river at points from 56 to 61 miles above the mouth of the river and representing a surface from 1,864 to 2,050 feet above the sea. In the ascent of the Río Coca from its mouth for 56 miles the rocks are all sedimentary. They descend progressively to rocks of older age because of a gentle eastward inclination of the strata. At a point 56 miles from the mouth of the river the base of the sediments is underlaid by igneous rocks, and as far upstream as we were able to continue, to a point about 61 miles from the mouth, these igneous rocks form the bed of the river which here occupies a deep gorge walled with cliffs of sedimentary rocks.

Since the base of the igneous rocks is not visible we do not know how thick they are or whether other sedimentary rocks underlie them or not.

The lowest of the igneous rocks, represented by samples 1–L and L–a, at elevation ±2,100 feet above the sea and about 61 miles from the mouth of the river, are volcanic fragmentals which occur as massive outcrops without any signs of stratification that we could see. Stratigraphically above these occur the rocks represented by sample No. 18, 60.5 miles above the mouth of the river, and by sample No. 2, secured at an elevation of 2,008 feet, about 59 miles above the mouth of the river.

A highly tuffaceous andesite (Specimen No. 6), from the lower falls of the Río Coca, about 58 miles from the mouth and at an elevation of about 2,000 feet, is found nearer the sediments.

Above this horizon, and represented by samples 1, 1-a, 2, 3, 4 and 5, collected at an elevation of 1,936 feet, about 58 miles from the mouth of the river, are altered trachy-andesite or latite, latite tuff, an acid volcanic tuff, a spherulitic felsite, a volcanic tuff of about trachy-andesite make-up and a modified basalt. At this point the rocks are very massive, slightly stratified, and jointed.

The rock immediately underlying the sediments (No. 17) is a basaltic andesite.

Since nothing has been known heretofore of the geology of the isolated region from which these samples come, brief petrographic descriptions of them may be of some interest.

Samples 1-L and L-a were taken farther up the canyon of the Río Coca and from a stratigraphically lower horizon than any of the other specimens of this series. They are very fine textured, strongly indurated, rocks and slightly weathered along joint surfaces. No. 1-L is gray and carries minute crystals of pyrite distributed along the joint planes. No. L-a is

dark and very fine textured, but neither of them reveals its true character megascopically, because of changes brought about by the intense hydrothermal attack to which they have been subjected.

Both of these rocks are volcanic fragmentals, but they differ somewhat in the nature of the fragments comprising them. No. 1-L is composed of acid volcanic glass fragments, including pieces of glass that are pumi-
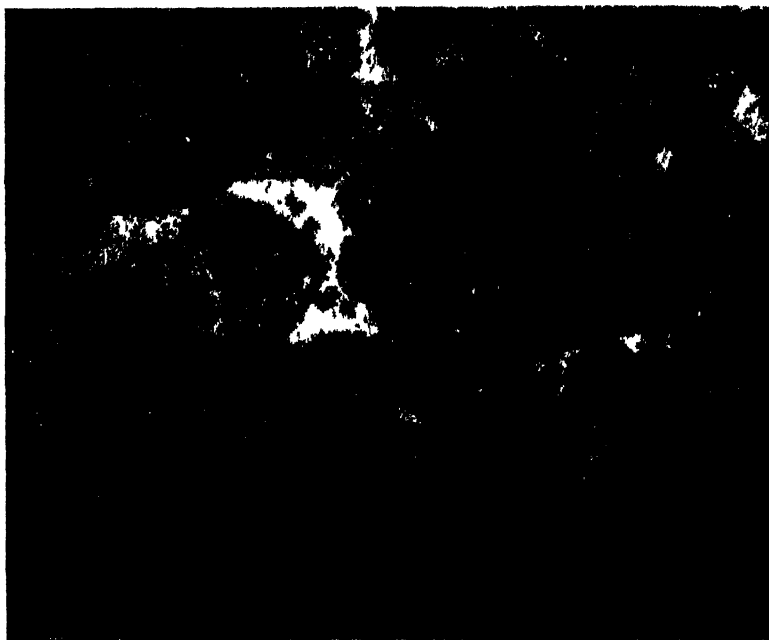
FIG. 9.—*Río Ooca 1L.*—Devitrified acid volcanic tuff. Photomicrograph, ordinary light, showing clastic character. Note pearlitic glass fragments, and other glassy lava fragments. The black streak cutting the rock is an interrupted veinlet of pyrite. × 31.

ceous, obsidian fragments with characteristic flow structure, pieces of pearlitic glass, and pieces of vitrophyre and other rock fragments, as well as many broken and much modified fragments of alkali feldspar and acid plagioclase. Crystals of magnetite and apatite are associated with some of the lithic fragments and veinlets of perfectly fresh pyrite cut all the structures in the rock, transecting many of the magnetite grains. All of the lithic and mineral fragments are closely packed in a small amount of groundmass that consisted initially of acid glassy ash, now thoroughly devitrified. In addition to the devitrification product

of the finer glass particles, chlorite, hematite, dusty and granular magnetite, quartz and leucoxene have developed as alteration effects.

The rock has been fractured likewise, and quartz, albite and pyrite were introduced. It is a devitrified, acid, volcanic tuff. Figure 9 illustrates the fragmental habit and the nature of the fragments.

Sample No. L-a was initially a fine acid ash, carrying small, broken and angular pieces of quartz and both alkali and acid plagioclase feldspar. The chief modification product is a quartzose and feldspathic devitrification aggregate, although a little leucoxene, chlorite and sericite have likewise been produced. The texture has been coarsened by devitrification and many wholly modified remnants ("ghosts") of shards of volcanic glass are distributed through the rock. It is a devitrified volcanic ash.

Specimen No. 18, from the next stratigraphically higher horizon and from a point 60.5 miles from the mouth of the Río Coca, elevation 2,050 feet, is a strongly modified, indurated and slightly tuffaceous rock with trachytoid groundmass, whose phenocrysts consist of both acid plagioclase and alkali feldspar, some of which show partial saussuritization; whereas in others, zoisite, epidote, sericite and albite occur in separate individual grains and patches. In this specimen, also, the general groundmass is extremely patchy and different in aspect from place to place, yet aside from the obvious lithic fragments, which are much altered but readily recognizable as distinctly different lithic units, the various unlike areas in the groundmass merge into one another by imperceptible gradations. Thus, despite the patchy behavior, the rock appears to be of definitely pyrogenic rather than pyroclastic origin. The rock carries larger crystals of magnetite and apatite than the other rocks of this series. Small crystals of pyroxene, but of phenocrystic dimensions, are completely altered to serpentine, and in rare instances to a mixture of quartz, epidote, zoisite and serpentine. The rock is intermediate between the trachytes and andesites. It is a porphyritic latite or trachy-andesite, modified and indurated.

Sample No. Z, from 60 miles above the mouth of the Coca, elevation 2,008 feet, represents a horizon nearer the sediments. It is a porphyritic rock with flow structure, initially of andesite make-up, but now completely modified and strongly indurated. The original, moderately basic, plagioclase phenocrysts are composed of mixed aggregates of coarse sericite, granular calcite, quartz, albite and epidote, all forming aggregate pseudomorphs after the original feldspar. Phenocrysts, of original hornblende that initially was resorbed along the margins, have been altered

to a mixture of calcite, epidote in fan-like, radiate acicular groups and a little quartz, all pseudomorphous after the former hornblende. The structures of the former resorbed margins are preserved as pseudomorphs composed of an opaque-white substance; this may be leucoxene derived from the alteration of possibly titaniferous granular magnetite that was formed during the resorption of the original hornblende.

The small plagioclase laths in the groundmass are likewise faithfully reproduced as mixed aggregate pseudomorphs, similar to the much larger phenocrysts of feldspar.

Patches of carbonate, containing perhaps a little iron and magnesia, in addition to lime, and small irregular areas of secondary aggregate-quartz, are scattered through the groundmass, products of the altera-tion of portions of it, and interstitial to the small groundmass feldspars. The rock contains also small irregular areas filled with chlorite and mosaic quartz, which suggest that leaching and filling were operative among the secondary processes which have affected the rock so profoundly. Most, if not all, of the primary substances have been destroyed. A few minute apatite crystals and euhedral grains of possible primary mag-netite are the only originals remaining.

The rock consists now of coarse sericite, albite, quartz, calcite and other carbonate, epidote, zoisite, chlorite, leucoxene and a little hematite. The striking thing is the retention of the former structures in the rock notwithstanding the complete change of its substance. It is a meta-andesite.

Specimen No. 6, from a massive outcrop at the lower falls of the Río Coca, 58 miles from the mouth, elevation 2,000 feet, represents the next horizon of these igneous rocks nearer to the sediments. This rock is so variable in texture from place to place that it is suggestive of a volcanic fragmental, but while there are a few distinct lithic fragments whose com-position is different from the main part of the rock, most of the mass is andesitic. The groundmass changes in quality gradually; in some places there is a distinct pilitic structure common to andesites; other places ex-hibit a fine granular structure, and still other portions of the rock are more coarsely pilitic with good flow structure. All of these apparently different units grade into one another so there are no distinctly outlined individual fragments with the exception of those previously mentioned. It is difficult to say whether the rock was initially a volcanic tuff of somewhat uniform andesitic make-up, whose separate fragments have been obscured through alteration, or whether it is an andesitic lava that is strongly xenolithic and whose caught-up fragments have not only been

sufficiently worked over to have lost their sharp outlines, but also still more obscured by alteration. The general aspect presented by the rock is that of a lava crowded with inclusions, some of which may be cognate inclusions, whereas others are distinct xenoliths of basaltic composition. These latter contain beautiful aggregate pseudomorphs of granular (mosaic) quartz after both pyroxene and olivine mixed in some cases with a little serpentine, and very irregular patches representing former cavities made by leaching, now filled with matted, acicular, greenish serpentinous aggregates that are almost isotropic, surrounded with much more strongly anisotropic matter that is composed of a mass of minute, interlocking scales, very much like fine sericite or talc, the whole margined with a very narrow strip containing fibers set perpendicular to the walls, resembling chrysotile in habit. Some of the patches carry feldspar phenocrysts which have been in part altered to quartz, sericite, zoisite-epidote and albite, and occasional phenocrysts of feldspar contain channels, formed perhaps by leaching, filled with the same fine serpentinous aggregate just described.

More or less leucoxene, granular titanite, chlorite, magnetite and limonitic matter are distributed through the rock in finely granular aggregates. The sample represents either a strongly indurated and modified, but remarkably uniform, andesitic tuff, or a highly tuffaceous andesite. It is probably the latter.

Comment on Analysis: A comparison of the chemical analysis of this rock with the average analysis of twelve andesites shows that both silica and alumina are appreciably higher in Río Coca No. 6, and both lime and magnesia are considerably lower. There is less than half the amount of lime in the Río Coca sample than is shown in the average andesite, and approximately but three-fourths as much magnesia. While the potash and soda, lower and higher respectively in the Río Coca sample, differ from the average andesite, they are nevertheless within the range of variation shown by the andesites themselves. The total iron content is higher in the average andesite, and manganous oxide lower; the greater part of the iron in the Río Coca sample is present in the higher state of oxidation, and the manganous oxide is rather high. Considering the altered condition of the rock, it corresponds fairly well with the composition of andesites in general.

The next higher horizon in these igneous rocks is represented by samples Nos. 1, 1-a, 2, 3, 1 and 5, from a point 58 miles from the mouth, elevation 1,936 feet. The outcrop is massive, possibly slightly stratified, jointed, and containing inclusions. They are all intensely altered, a con-

dition common to every one of the Río Coca samples. Nos. 1 and 1-a represent material a few feet higher stratigraphically than Nos. 2 and 3.

Sample No. 1 is very slightly porphyritic, with a trachytoid fabric, the feldspars consisting of plagioclase laths distributed among crystals of alkali feldspar that are somewhat larger than the plagioclase laths, but not of phenocrystic dimensions. All the feldspar is altered. Sparingly distributed granules of former pyroxene have been converted into a mixed modification-aggregate consisting of serpentine and chlorite. The rock is essentially an altered trachy-andesite, or latite.

Specimen No. 1-a is much more obscure. It carries feldspar crystals that seem to be phenocrysts, but the rock is either strongly tuffaceous or else a real fragmental. The phenocrysts of feldspar are chiefly of the alkali type, although acid plagioclase is present among them. All of them are more or less sericitized, and occasionally granules of epidote appear as one of their modification products. Many of them exhibit a streaked and patchy appearance common to feldspar that has been partially albitized, and these feldspars are judged to have been modified by sericitization, albitization and, to a very slight degree, by epidotization.

The groundmass of the rock is extremely variable, changing in texture, structure and in composition from place to place. Some areas exhibit typical hyalopilitic structures characteristic of andesites; other places are finely felsitic, almost glassy, with minute feldspars and fragments of crystals distributed in them; and still other areas, felsitic or finely granular, carry feldspar phenocrysts themselves, suggesting fragments of a porphyritic volcanic of some sort. Yet, with a few exceptions, these areas are not sharply outlined; they have all been obscured through alteration and they merge imperceptibly into one another.

Coarsely crystalline epidote, mixed with zoisite and quartz, forms aggregate pseudomorphs after pyroxene, both single and grouped; the grouped pseudomorphs carry numerous included euhedral grains of magnetite.

There are indistinctly outlined areas in the rock composed of epidote and zoisite, suggestive of possible basic lithic fragments that have been completely destroyed by alteration; and non-pleochroic, light-green serpentine aggregates pseudomorphous after forms suggestive of hornblende.

The rock is judged to be a very much altered, strongly indurated, obscurely fragmental or strongly tuffaceous volcanic with the composition of trachy-andesite or latite; essentially it is an extensively altered, tuffaceous and porphyritic latite. Figure 10 illustrates this rock.

Specimen No. 2 is lower stratigraphically than No. 1, and pyroclastic in origin. It is composed of fragments of obsidian with flow structures, pieces of pearlitic glass, and fragments of vitrophyre and keratophyre, all very much altered. Many broken crystals of both alkali feldspar and plagioclase are contained in the rock, some partially, others almost completely, altered to mixed aggregates consisting of sericite, patches of albite and granular epidote. Considerable epidote and a little calcite occur all through the rock, and much mosaic quartz has developed
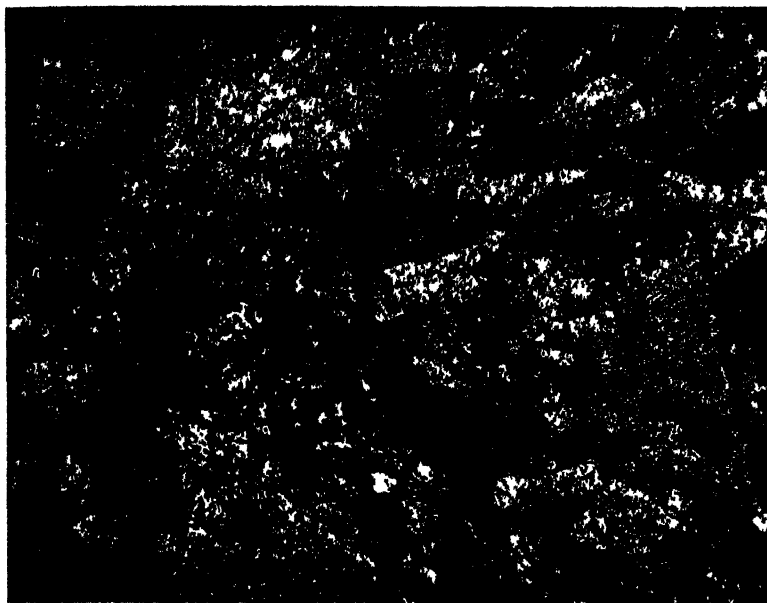
Fig. 10. *Rio Coca No. 1a.* Tuffaceous and porphyritic latite. Photomicrograph, ordinary light, showing the very obscurely fragmental habit, porphyritic structure and groups of partially albitized feldspar phenocrysts. The rock is highly variable in texture and groundmass habit from place to place and very strongly tuffaceous, but the fragments or xenoliths are so much modified that they merge into one another, and are only indistinctly outlined. ✕2ł.

through the silicification of some of the lithic fragments whose former pearlitic, pumiceous and flow structures are retained only as "ghost" or inherited structures. Minute fractures in the rock are filled with quartz, calcite and epidote.

It is an indurated, intensely modified, moderately acid volcanic tuff, with the composition of a trachyte or latite.

Specimen No. 3, taken from the neighborhood of No. 2, is a fine,

thoroughly devitrified, spherulitic felsite; probably a devitrified spherulitic glassy lava originally, fractured and healed with quartz, which not only fills the fractures but which also encroaches on the substance of the rock as well. The primary spherulitic structure exists now as a relic or "ghost" structure, since the rock has been very extensively modified.

Specimens Nos. 4 and 5, taken from the same vicinity as Nos. 1, 1-a, 2, and 3, are different in initial make-up, although they have suffered in the same way as the others from intense hydrothermal attack. *Sample No. 4* is of pyroclastic origin, carrying many fragments of various sorts of igneous rock, ranging from acid pearlitic lavas to pieces of andesitic rock, and fragments of broken feldspars. All the fragments are much altered; chlorite, serpentine, epidote, quartz, magnetite and leucoxene are the dominant secondary substances, and the rock has also been silicified to some degree through the introduction of quartz.

The original clastic character of the rock has been considerably obscured by these changes; the same set of products has developed in the initially fine groundmass in which the lithic fragments are distributed, and rather extensive devitrification has likewise been brought about. It is essentially a much modified volcanic tuff of about trachy-andesite make-up.

Sample No. 5, from the same vicinity as No. 4, is very different from No. 4 and from all the preceding samples of the Río Coca series. It is very strongly porphyritic, the larger phenocrysts consisting of augite, much fractured within the crystals, which contain areas that are somewhat granular. The augite crystals have a habit of close grouping, so that aggregate or compound phenocrysts composed of closely knit but differently oriented units result.

The birefringence of the augite does not exceed 0.030, the pleochroism is imperceptible and $Z_\wedge c$ is approximately 45°. Some of the augite crystals are wholly altered, others only slightly altered; the alteration products are epidote, quartz, penninite and calcite. Penninite, occasionally mixed with a little calcite and quartz, likewise occurs pseudomorphous after olivine; the crystals (pseudomorphs) are smaller than the augite and frequently sharply idiomorphic.

The plagioclase, both as phenocrysts and as small laths distributed in the groundmass, is labradorite. It has been more or less modified, however, so that it consists in part of alteration aggregates composed of fine mixed sericite, epidote, carbonate, and zoisite.

Interstitial basic glass forms part of the groundmass of the rock, but it appears opaque white in thin section, consisting now of one of the

kaolin minerals, probably anauxite. The general character of the rock is shown in Figure 11; the black interstitial groundmass is really opaque white by reflected light. The rock is a modified basalt.

Specimen No. 17. Immediately underlying the sediments occurs igneous rock presented by Sample No. 17, collected at a point 56.5 miles from the mouth of the Río Coca, at an elevation of 1,864 feet. The outcrop is massive and vein-streaked. This very fine textured black rock
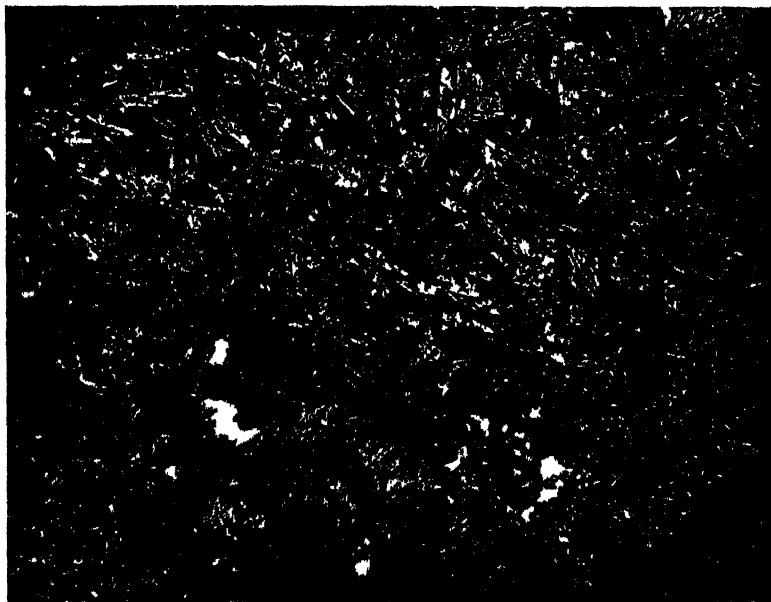
Fig. 11. *Río Coca No. 5.* Modified Basalt. Photomicrograph, ordinary light, showing strongly modified feldspars, and aggregate pseudomorphs of epidote, quartz, calcite and penninite after augite (in the lower part of the picture). The black groundmass in which all the crystals are distributed is basic glass, now partially altered to an opaque white product judged to be anauxite ×24.

is slightly porphyritic, with a beautful fluxion structure emphasized by microlites of labradorite, which are not greatly modified, set in a mesostasis of glass. The phenocrysts consist of colorless pyroxene, resembling in optical and structural characters that described as occurring in Sample No. 5; and mixed pseudomorphs of limonite, carbonate and chalcedony after olivine.

As in Specimen No. 5, several units of pyroxene form closely knit groups, each individual of the group having a different orientation, making compound phenocrysts. In most cases several, sometimes each one,

of these units have been partly altered to clear granular carbonate, probably calcite, different in appearance and behavior from the carbonate that is contained within the destroyed olivine crystals and which is distributed in patches all through the groundmass of the rock in the form of a very finely granular aggregate with a turbid aspect, quite unlike the large clear calcite grains in the pyroxene. A number of small fractures, filled with later mosaic-quartz and calcite, transect the rock, cutting
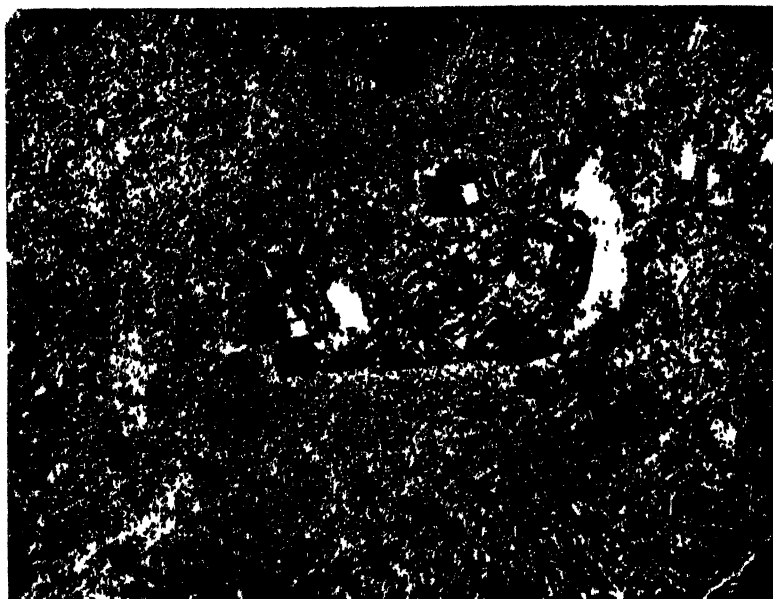
Fig. 12.—Río Coca No. 17.- Basaltic andesite. Photomicrograph, ordinary light, showing tiny labradorite microlites in fluxion structure, and one of the completely altered olivine phenocrysts. These consist of mixed aggregates of limonite, carbonate and chalcedony, pseudomorphous after the original olivine. ×24.

through groundmass, carbonated patches in the groundmass, and phenocrysts, indifferently. The specimen is on the border between andesites and basalts; it is strongly feldspathic and possesses the characteristic hyalopilitic fabric of andesite, but the ferro-magnesian components are pyroxene and olivine and the feldspar is labradorite. It is essentially a basaltic andesite. Figure 12 illustrates this rock.

Río Misahualli Series

About sixty-two miles in an air-line southwest of the Río Coca volcanics, and also underlying almost-horizontal sediments, some of them

of proved Albian age, there is another series of altered volcanics of un-
known thickness; their base is not exposed. These outcrop in the bottom
of another deep canyon, that of Río Misahualli, at an elevation of about
1,500 feet.

About 100 feet of these rocks are exposed at the river surface. At
this locality marine limestones of Albian age are separated from the under-
lying volcanics by about 100 feet of sandstone, which is absent on the
Río Coca at the same horizon. We do not know whether any pre-Albian
sediments are represented here or not. As in the Río Coca series the
underlying volcanics represent flows and tuffs, now greatly altered, all o'
which are certainly much older than the Albian.

Sample No. 73. The rock immediately underlying the sediments and
corresponding in horizon to the basaltic andesite (Specimen No. 17) of
the Río Coca, is exposed in cliffs composed of massive grayish-pink to
yellowish streaked rock. The sample, which was collected on October
11, 1921, was secured from a place about three miles below the mouth
of the Río Hollín.

The specimen is somewhat obscurely fragmental and considerably
altered. The most conspicuous fragments are those in which alteration
has produced both hematite and limonite; these stand out sharply from
the more obscure fragments in which alteration has taken other forms.

The fragments consist of andesite, whose interstitial groundmass is
thoroughly altered and heavily charged with hematite, and whose felds-
par microlites are also modified; altered pieces of vitrophyre, some charged
with hematite, others stained by limonitic products, pieces of much altered
basaltic vitrophyre, pieces of keratophyre not so badly modified, pieces
of dacite carrying phenocrysts of plagioclase and small corroded pheno-
crysts of quartz; broken crystals of orthoclase, slightly sericitized, large
crystals of plagioclase of oligoclase-andesine composition, usually more
or less fractured, slightly sericitized, stained with limonite and charged
with hematite; thoroughly altered biotite crystals and broken hornblende,
almost completely converted to mixed hematite-limonite; and much
secondary quartz in fine grains and patches of fine mosaic-like aggregates.
Crystals of modified titanite and limonite pseudomorphs after pyrite are
sparingly distributed through the general groundmass. The rock as a
whole is stained with limonite and contains streaks and patches of hema-
tite, kaolinitic matter and leucoxene.

It is difficult to classify a mixed fragmental of this character; the aver-
age composition of the rock is judged to be intermediate between the

rhyolites and dacites, and for all practical purposes it may be regarded as a very much modified dellenitic tuff.

Figure 13 shows one of the more conspicuous fragments, that stands out prominently from the more obscure fragments surrounding it.

Specimens A and 69 were collected immediately underneath the dellenitic tuff (Sample 73) just described, two miles farther up the Misahualli river, and about one mile below the mouth of the Hollin river.

Fig. 13   *Rio Misahualli No. 73.*   Dellenitic tuff.   Photomicrograph, ordinary light, showing one of the more prominently outlined andesite fragments, and other fragments very much more obscure, owing to the extensive alteration.   The small white patch on the right of the large fragment is quartz.   × 24.

Sample A has a finely felsitic groundmass in which microphenocrysts of feldspar are distributed.   Orthoclase, microperthite, and plagioclase that has the composition of oligoclase-albite, as nearly as could be determined, are all represented among the tiny feldspar crystals.   They have all been more or less modified.   Ferromagnesians are almost lacking in the rock; the few crystals consist of bleached biotite carrying little granules of zoisite and patches of leucoxene.

Very small xenoliths are sparingly scattered through the groundmass, which is somewhat variable in habit from place to place, but this feature

is rather obscure owing to alteration and to the development of fine secondary quartz.

The rock is undoubtedly tuffaceous, if not actually fragmental; it has the general composition of a trachyte, but it lacks the structure characteristic of true trachytes. It is essentially an exceedingly fine textured, altered and tuffaceous trachytic felsophyre, or possibly a modified and strongly indurated trachytic ash.
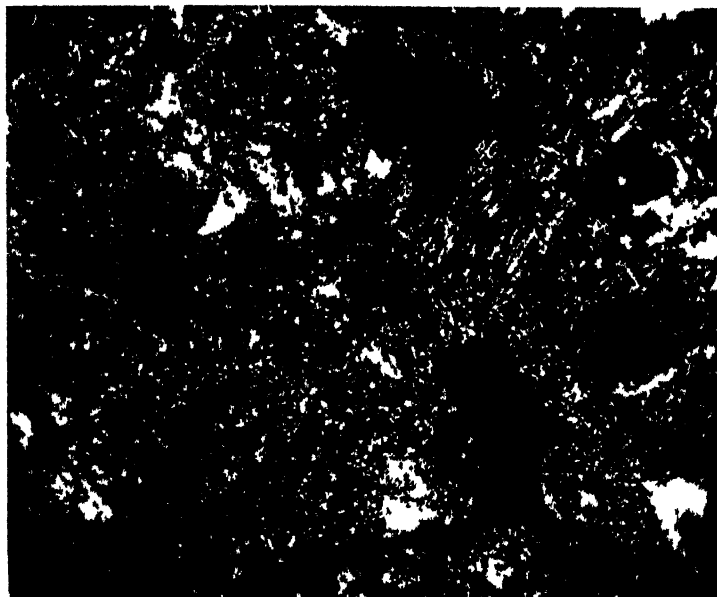
FIG. 14   *Rio Misahualli No. 1*   Indurated, altered tuffaceous trachytic felsophyre Photomicrograph, nicols crossed, showing the strongly silicified condition of the rock Most of the small white specks are quartz of secondary origin. The larger white patches are feldspar, the black ragged patches are holes in the section. ×60

The fine texture of the rock, its altered condition, and the abundance of fine secondary quartz, are shown in Figure 14.

Sample 69 is also finely felsitic, with a few small completely kaolinized microphenocrysts of feldspar and an occasional bleached and completely modified biotite crystal distributed through the groundmass, which is composed almost wholly of a micro-granular, interlocking aggregate of alkalic feldspar, minutely micrographic in places, very slightly sericitized, containing minute, scattered patches of carbonate and a little secondary ' quartz.

The rock is veined with calcite with which is associated a little pyrite and what appears to have been siderite that has been entirely altered to mixed red-black hematite and to carbonate.

This sample is essentially the same as Sample A in general composition, but the groundmass is much more uniform both in structure and texture, and there is no suggestion of fragmental habit at all. It is essentially a trachytic felsophyre.
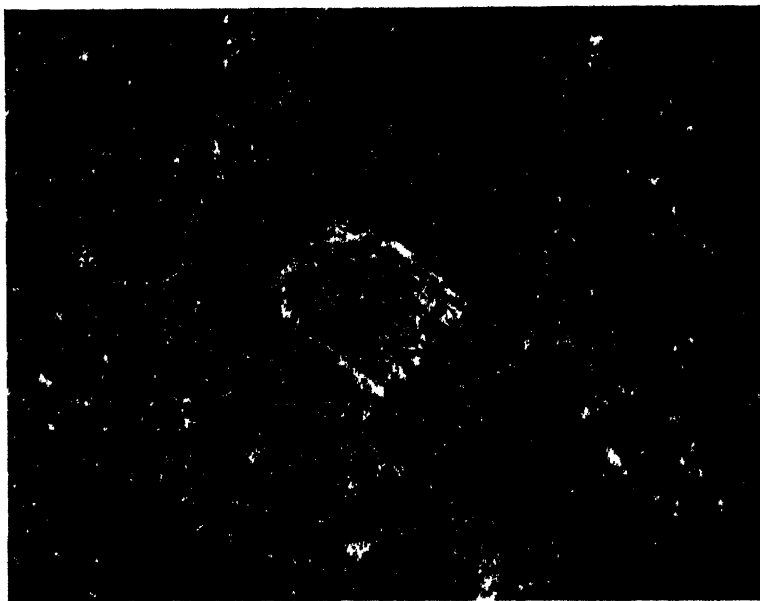
FIG. 15.—*Rio Misahualli No. 69.*—Altered trachytic felsophyre. Photomicrograph, nicols crossed, showing altered feldspar phenocryst and microgranular groundmass of feldspar. ×60.

Some of the features mentioned are illustrated in Figure 15, which shows the microgranular character of the groundmass and one of the kaolinized and slightly sericitized little feldspar crystals.

Specimens 71, 71a, 71b and 72 represent the lowest formations, stratigraphically, encountered on the Misahualli river. The samples were taken from an outcrop along the river about two miles below the mouth of the Hollin river. The rocks here dip 10° west, upstream. In the field the weathered exposure strongly resembles a conglomerate, containing rounded "pebbles" up to two or three inches in diameter. These "pebbles," however, proved to be amygdaloidal fillings in an originally extremely porous basalt.

Samples 71, 71-a, 71-b are different specimens taken from the same formation.   The rock is composed of small plagioclase laths and somewhat larger crystals of the same substance, all very considerably modified.   The alteration is saussuritic in character, consisting of patches of sericite, chlorite and excessively finely microgranular zoisite distributed in new and more acid feldspar than that which originally composed the laths.
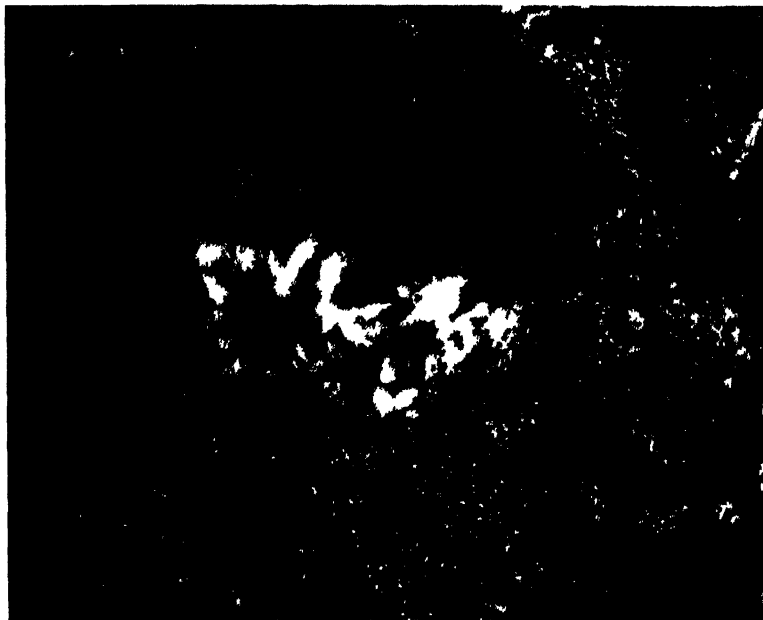
FIG. 16. *Río Misahualli No. 71.* Altered basaltic amygdaloid. Photomicrograph, nicols crossed, showing ovoid or lenticular amygdule of aggregate quartz, quartz pseudomorphous after pyroxene, completely altered feldspar and dark altered glassy groundmass. ×21.

Much larger crystals of phenocrystic dimensions have been altered to mosaic-like aggregates of quartz, mixed with faintly green mica, the whole forming beautifully pseudomorphic aggregates after what is judged to have been originally pyroxene. Small olivine crystals, now consisting of an alteration complex of various forms of serpentine, mixed with carbonate, are sparsely disseminated through the groundmass, which consists of brown basic glass, in which all of the altered crystals mentioned above are distributed. Some of the vesicles are filled with quartz in the form of both mosaic-like aggregates and feathery chalcedony, mixed, in

some cases, with carbonate and zeolites, and others are filled with carbonate.   Quartz and chalcedony form the major part of the fillings, so that the round and ovoid amygdules, being much more resistant to weathering than the rock itself, have weathered in relief, thus giving the rock the aspect of a conglomerate in the field.

Little cubes of pyrite, some still unaltered, others partially and wholly converted to limonite, are associated with the mosaic-like quartz aggregates pseudomorphous after pyroxene previously mentioned, and veinlets of mixed quartz-chalcedony traverse the rock, containing as part of the mixed vein-filling a black metallic mineral of some sort not determinable in thin section.   Extremely irregular cavities, evidently produced by leaching, are also filled with the quartz-chalcedony aggregate similar to that which occupies the primary vesicles.   The brown, basic, glassy groundmass is itself altered to a translucent product, white by reflected light, and presumably of kaolinitic nature, although the "glassy" groundmass is still brownish in color by transmitted light.

The rock is an altered, glassy, basaltic amygdaloid, rather uncommonly vesicular originally, containing abundant amygdules of considerable size.

Sample 72 (a-b and c) was secured in the same locality as Sample 71, and represents the same formation.   It is similar to No. 71 in composition, structure and alteration effects, but carbonate as a secondary product is much more prominent than in No. 71.   Irregular leaching cavities, now filled, are more numerous in this sample, but the rock is not much different otherwise.

The plagioclase is greatly altered and original pyroxene and olivine are entirely destroyed; they are represented now by complex aggregate pseudomorphs consisting of quartz, carbonate, serpentine and limonitic products, and the initially glassy groundmass is more or less kaolinized and stained with limonite.   Figures 16 and 17 illustrate different specimens of this rock.

Río Jandache Series

The third place where the base of the sediments and the underlying igneous rocks were encountered is about 20 miles north of the occurrence on the Misahualli river and about 50 miles in an air line southwest of the Coca river locality.

Here the sediments terminate against the Guacamayos mountains at an elevation of 4,000 feet above sea level.   They form cliffs in the valley of the Jandache river where the trail from Quito to the Napo river crosses the valley.

The presence of these sediments, and the underlying igneous rocks similar in character to the volcanic rocks and associated overlying sediments found at the Coca river and the Misahualli river, afford additional evidence of the existence of a widely distributed sedimentary series lying unconformably on a series of much older, altered igneous rocks of surface volcanic types.
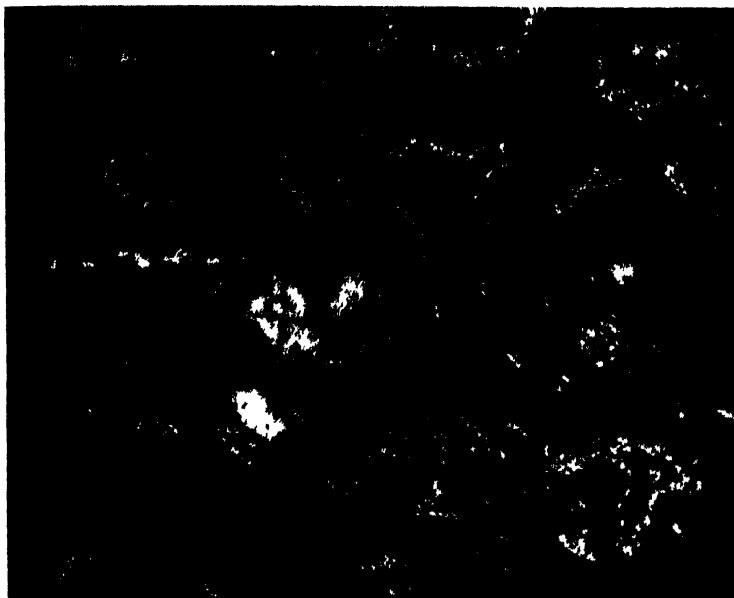
FIG. 17. *Rio Misahualli No. 73b.*--Altered amygdaloidal basalt. Photomicrograph, nicols crossed, showing cavities formed by leaching, filled in part with calcite, in part with fine serpentinous matter; and completely altered feldspar laths distributed in an altered, dark, glassy base. X21.

Specimen B, collected from the cliffs and beneath the sediments of the Jandache river, is a spherulitic, porphyritic and devitrified lava, with a composition intermediate between a rhyolite and dacite.

The rock was initially a porphyritic glass containing spherulites, small phenocrysts of oligoclase and orthoclase, little biotite crystals now thoroughly bleached and spotted with magnetite, limonite, leucoxene and hematite, and multitudes of crystallites distributed through the originally glassy groundmass in swirling flow lines. The primarily glassy groundmass consists of an unusually coarse and intricately interlocked devitrification aggregate composed of quartz and feldspar, which retains traces of

replaced spherulites and through which the lines and streams of crystallites pass uninterruptedly.

The feldspar phenocrysts are slightly kaolinized and flecked with tiny scales of sericite, and a few small hornblende crystals in the groundmass have been so thoroughly destroyed by the alteration attack that only their
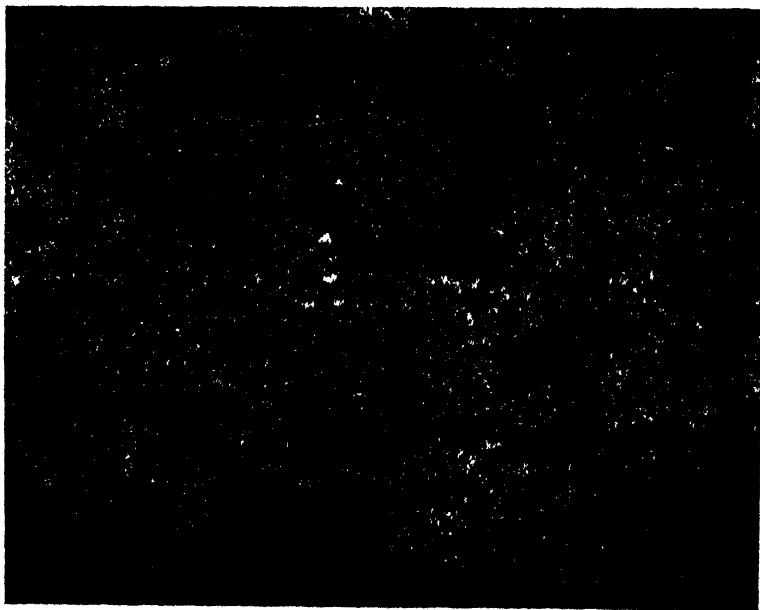
Fig. 18.—*Río Jandache No. B.*—Devitrified altered dellenitic vitrophyre. Photomicrograph, ordinary light, showing fine and originally glassy microlitic groundmass, with flowage and traces of spherulites, and an altered orthoclase phenocryst. ×25.

outlines remain. They consist now of an aggregate of quartz mixed with a little fine flaky mica and limonite. The rock is a coarsely devitrified dellenitic vitrophyre. Some of the features mentioned are shown in Figures 18 and 19.

B. IGNEOUS ROCKS OF PROBABLE PRE-ALBIAN AGE

Río Pastaza Series

In the gorge of the Pastaza river, between the mouth of Río Topo, which lies at an elevation of 4,000 feet, and the hamlet of Mera, 3,800 feet above sea level, 47 miles and 56 miles, respectively, by trail from the city of Ambato, there is a narrow belt of igneous rocks nine miles in width,

lying between exposures of sediments, on the one end at the mouth of the Topo River and on the other just east of the village of Mera.

The sediments at Topo river are limestones, shales and sandstones, containing fossils. A good collection of these was made but it was unfortunately lost in transit. We believe these rocks are Cretaceous. They dip westward at an angle of 55°, striking nearly north-south. The sediments just east of the village of Mera are Cretaceous.
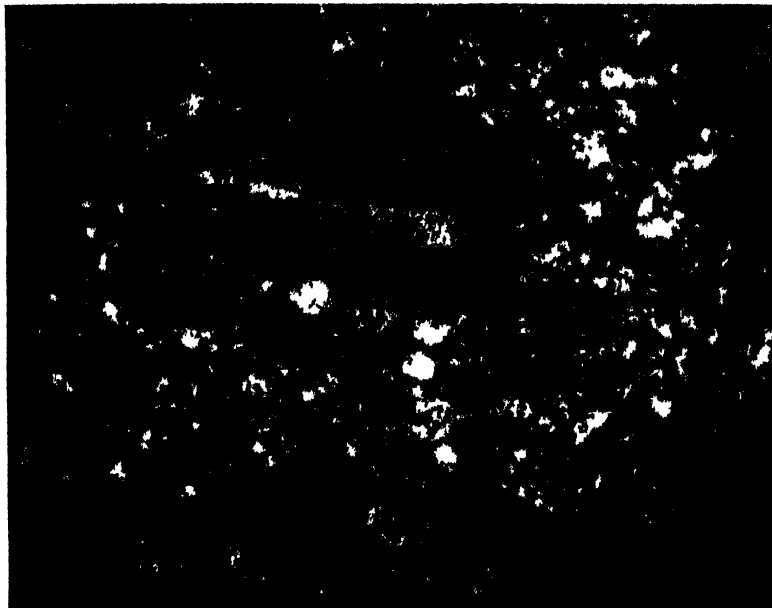
Fig. 19.—*Río Jandache No. B.*—Photomicrograph, same field seen in Fig. 18, nicols crossed, showing complete devitrification of the former glassy groundmass, and altered phenocryst of orthoclase. ×21.

On the east bank of the Topo river there are blocks of reddish granite, and exposures of this granite occur in Zunac creek, which lies a mile to the east. The granite may be traced as far as a hut called "Tamba de Cashaurcu," 7.75 miles by trail from the Topo river, and lying at an elevation of 4,674 feet above sea level. In the midst of the granite, which apparently forms the surface almost as far as the village of Mera, and between a high ridge to the eastward known as Abitagua and a point about one and a half hours' walk from the hut called Cashaurcu, there is an outcrop of igneous rock of surface volcanic type, resembling the previously described pre-Albian rocks of the Coca, Misahualli and Jandache rivers.

Since this exposure is not directly associated with any of the sediments
the age of these volcanics is unknown.

Specimens 7a and 7c were secured from the exposure mentioned, on the
north side of the Pastaza Valley about three miles west of Mera.

Sample 7a is coarsely felsitic in texture. It is composed of dominant
alkali feldspar and quartz in beautiful micrographic intergrowths, occa-
sional slightly larger individual allotriomorphic quartz grains and small
patches of mosaic-like aggregates of quartz, the whole forming over 95
per cent of the rock. Tiny shreds of chloritized biotite and a few chlori-
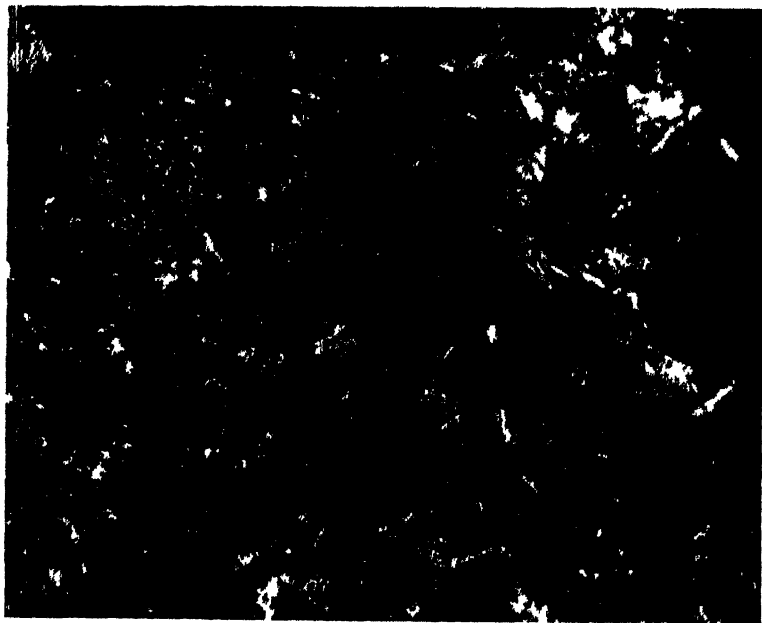
FIG. 20.—*Pastaza Valley No. 7a.*—Rhyolite. Photomicrograph, nicols crossed, show-
ing finely micrographic quartz-feldspar groundmass containing small euhedral laths of
oligoclase in the micrographic areas, and anhedral grains of quartz. ×60.

tized crystals of the same mineral, of phenocrystic dimensions, are scat-
tered through the groundmass, together with a few small aggregate patches
of zoisite-epidote. The most striking thing about the rock is its micro-
graphic structure. Minute euhedral crystals of plagioclase feldspar, of
acid oligoclase composition, are set in poikilitic fashion in individual
micrographic areas, different sections of which extinguish differently, so
that the micrographic units simulate crude and extremely coarse spheru-
lites.

In composition the rock is a rhyolite, although it lacks flow structure.

Sample 7c is finer textured than No. 7a, and lacks the very striking micrographic structure displayed by that specimen. The groundmass consists of a closely interlocking fine aggregate of alkali feldspar, carrying numerous fine scales of sericite. Both orthoclase and acid oligoclase occur as phenocrysts, as well as corroded quartz crystals. A few bleached biotite crystals spotted with little patches of leucoxene represent the only other component in the rock. Like No. 7a, this specimen is a simple rhyolite, lacking flow structure. Figures 20 and 21 illustrate these two rocks.

"Cordillera" Guacamayos Series

Specimen A, B and C.—About twelve miles, in an air line, south of the village of Baeza on the trail to the Napo River there is a prominent but narrow ridge whose crest rises to an elevation of 7,870 feet above the sea. Six miles south of this summit, at the base of the ridge, the trail crosses the Río Jandache where, as previously mentioned, the pre-Albian sediments terminate in the south slope of the valley and are underlain by altered volcanics.

The rocks of the "Cordillera" Guacamayos, probably of the same age as the pre-Albian volcanics, are badly weathered, rusty, brown and white mottled, and contain chalky white spots.

Although *Specimen A* is very much altered there are distinct traces left of its former texture and structure. It is coarsely porphyritic, with large phenocrysts of altered plagioclase feldspar and Carlsbad twins of alkali feldspar distributed in a moderately coarsely crystalline groundmass composed of smaller laths of altered plagioclase, and plates of bleached biotite. Larger crystals of biotite, of phenocrystic dimensions, are likewise distributed through the rock. Most of the feldspar is thoroughly altered; all of it has been sericitized and a great deal of it has been albitized. The rock has been flooded with quartz and albite to such a degree that the original groundmass-feldspar laths, now almost wholly modified in composition, are distributed in a much coarser textured mosaic of albite and quartz, which is filled with "dust" outlining the forms of the earlier replaced feldspar, and with bubble and liquid inclusions as well.

Here and there albite twinning may be observed in some of the feldspar phenocrysts, but the clear feldspars of the phenocrysts are crowded with bubble and liquid inclusions; this feldspar is judged to be later replacement albite. All the biotite is bleached, wholly or in large part, with the development of brilliantly polarizing colorless mica, a faintly green pleochroic mica that is also brilliantly polarizing, a little granular titanite,

granular magnetite, and a little leucoxene. Fine flaky chlorite is also a
product of the same process.

There is no evidence of crushing or shearing, but the rock is so thor-
oughly modified by processes that were under igneous control that provided
the extent of this sort of modification may be considered a criterion, this
rock belongs to the older group; that is, it is probably older than the late
Andean lavas (pre-Quaternary). Weathering has produced limonitic and

FIG 21.—*Pastaza Valley No. 7c*—Rhyolite. Photomicrograph, nicols crossed, show-
ing partially resorbed quartz phenocryst and groundmass of fine, interlocking micro-
crystalline aggregate of feldspar, more or less sericitized. ×60.

kaolinitic products, subsequent to the modification of the rock by the
metasomatic replacement by quartz and albite. A little of the quartz may
be primary, more especially in scattered areas where it has an interstitial
distribution. It is almost impossible to differentiate, however, between
original quartz and that which is associated with the albite as replacement
quartz. So far as can be judged, the rock is a much modified and exten-
sively weathered monzonite porphyry, or a closely related type.

Sample B.

This specimen carries phenocrysts of embayed quartz, in many instances
surrounded by and in all cases connected with and encroached upon by

very coarsely spherulitic feldspar, which is associated not only with the quartz phenocrysts but which also occurs in close connection with the feldspar phenocrysts as well. Very much smaller spherulites with the same composition are distributed all through the granular quartz-feldspar groundmass.

The feldspars, both as phenocrysts and in the groundmass, are almost completely altered; in part to fine flaky sericite; in part to an opaque-
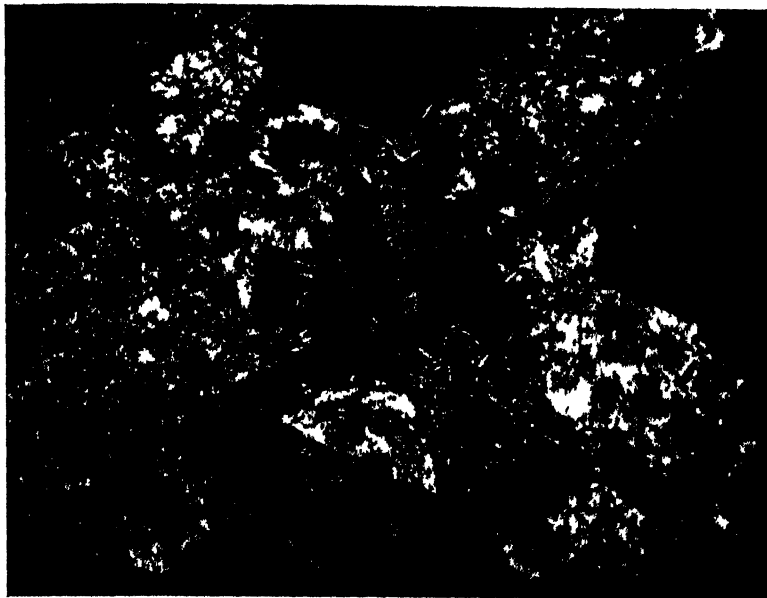
FIG. 22.--*Cordillera Guacamayos No. B.*—Spherulitic granophyre. Photomicrograph, nicols crossed, showing granular groundmass of quartz-feldspar, altered feldspar phenocrysts and a spherulitic area with center of quartz. The dark crystals at top and right of picture are altered, very turbid and sericitized phenocrysts of feldspar. The rock is strongly porphyritic. ×20.

white finely granular product that causes the feldspar to look very dark and turbid by transmitted light, probably a form of kaolinite ; and in part to a low index, transparent but milky isotropic substance that may perhaps be halloysite (?). The feldspars still show traces of both albite and Carlsbad twinning; they are judged to have been initially both orthoclase and soda plagioclase.

The biotite has been wholly destroyed and converted into aggregate granular pseudomorphs of quartz, epidote, chlorite, magnetite and leucoxene. Superficial weathering has been productive of limonite, which

has formed at the expense of some of the biotite, and which is likewise distributed in minute cracks in the rock. The halloysite (?) and the other opaque-white alteration product of the feldspars are likewise judged to be superficial weathering products. The rock is a spherulitic granophyre.

Figure 22, a photomicrograph taken with nicols crossed, illustrates the coarsely spherulitic character of the rock, its porphyritic habit, and the moderately granular condition of parts of the groundmass that are not spherulitic.

Sample C has been much more affected by weathering than either A or B. It is a granitoid rock whose feldspar, now almost completely destroyed, was a basic or moderately basic plagioclase. The original ferromagnesian has been entirely converted into a brilliantly polarizing, brownish yellow, slightly pleochroic fibrous and scaly aggregate judged to be goethite, which is distributed along the cleavages of the feldspar and in the body of the feldspar itself in fan-like groups of fibers, as well as interstitially. Much epidote and secondary quartz have developed through the alteration of the feldspars, so that the rock now consists largely of secondary aggregates and products of weathering. From the remnants of originals left and the nature of the alteration substances, the rock is judged to be a gabbro, or an allied type.

All of these samples are probably related to an earlier igneous stage than that which gave birth to the later lavas. There is no evidence, however, of any of the severe deformation that has affected the schist series of the Papallacta group.

Río Papallacta Volcanics (pre-Albian?)

In the midst of the schists of the Río Papallacta, 6.7 miles east of Papallacta, at an elevation of 8,571 feet, there is an outcrop of apparently the same formation as that underlying the Albian sediments.

Specimen 2b, representative of this outcrop, is a very fine textured, pinkish, and much indurated rock.

Although all the original minerals have been completely destroyed, both texture and structure are beautifully preserved. Some of the lath-like feldspar and some of the originally fine interstitial groundmass have been converted into a very fine microcrystalline aggregate whose index of refraction is higher than that of the associated quartz; it is judged to be microcrystalline kaolinite. The femic components of the rock have been altered to limonite and turbid carbonate, appearing in ragged patches but also pseudomorphous after small prismoids of some sort, probably either

augite or hornblende. The complete destruction of the components, but at the same time the preservation of their original form and distribution, is a very striking feature.

Much quartz of secondary origin is a prominent component of the rock, and this has replaced both groundmass and feldspar. Judging from the relations between the quartz and kaolinite the quartz is earlier; the kaolinite actually encroaches on the quartz and in many instances it has com-

Fig 23.—*Papallacta River Volcanic No. 2b.*—Photomicrograph, ordinary light, showing relic structure The feldspars are merely "ghosts" of original plagioclase laths. They are so completely replaced by quartz and kaolinite that all traces of them disappear between crossed nicols. The interstitial groundmass has been altered to fine microcrystalline kaolinite and quartz. The black patches are limonite   ×24.

pletely replaced the secondary quartz, so that the substance of the groundmass and former feldspars is entirely kaolinite; whereas in other areas the replacement of the quartz by kaolinite is partial, the former feldspars consisting of both products. In places where the quartz is the chief replacing medium, the lath-like feldspars are structurally suggestive of former plagioclase.

The rock was probably initially an andesite or some closely related type, which was thoroughly silicified and partially kaolinized. It is certainly later than the schists, but whether it may be related to some of the late Andean lavas or not it is impossible to say.

Figure 23, a photomicrograph taken in ordinary light, illustrates the feldspar forms, now completely altered. Between crossed nicols the relic structure, seen in ordinary light and shown in the photomicrograph, vanishes, a microcrystalline aggregate of quartz and kaolinite taking its place. It will be observed that the rock exhibits no signs of deformation at all and no evidence whatever of any of the intense deep-seated metamorphism that characterizes the schist series.

Río Quijos Samples (pre-Albian?)

We questionably assign to this category two samples from the Río Quijos, Nos. 11 and 12. These rocks are of doubtful origin and uncertain relations. Specimen No. 11 was secured along the road between Quijos bridge and the cable crossing over the Quijos River, one mile from Baeza, at an elevation of 5,870 feet. Sample No. 12 came from a massive outcrop on the left bank of the Río Quijos at the cable crossing, one-fifth of a mile north of No. 11 at 5,852 feet elevation.

No. 11 is a limestone breccia whose origin is obscure. It is composed of finely granular crystalline carbonate, carrying patches or fragments of very coarsely crystalline carbonate that presents evidence of severe crushing; and shattered grains and areas of quartz, transected by veinlets of carbonate.

Veinlets of carbonate cut the whole rock mass as well, intersecting, ramifying and forming a carbonate-filled fracture system in a carbonate rock that is itself a breccia.

No. 12 is a serpentinized rock of doubtful origin. It is composed of lamellar antigorite with heterogeneous grouping in places, as well as in rosettes, blades, fan-shaped leaves and fine aggregates. Occasional patches resemble bastite, possibly representing completely destroyed orthorhombic pyroxene. In addition there is a little fibrous anthophyllite (gedrite) and considerable carbonate with steel-gray interference colors that may contain iron and perhaps magnesia as well as lime. Irregular grains and groups of grains of magnetite and pyrrhotite are sparingly distributed through the rock, which contains no trace of any original structures unless the possible bastite areas connote former pyroxene crystals.

It is possible that this rock may have been derived from a basic igneous rock of the nature of a peridotite, but there is no definite proof of this in the sections.

(c) THE GRANITES

We have no information regarding the age of the granites of eastern Ecuador. We found them in three regions; one on the Río Pastaza, an-

other in the country south of the Guacamayos mountain ridge, between it and the Río Jandache, and a third on the Río Napo a few miles below Napo, where the granite has a peculiar occurrence.

Río Pastaza

Specimen 7b. Between the sedimentary rocks of Cretaceous age at the mouth of the Río Topo and in the vicinity of Mera, from 4,000 to 3,800 feet above the sea, there is a mass of red granite which is several miles wide

FIG. 24.—*Río Pastaza granite.*—Photomicrograph, nicols crossed, showing graphic structure. Over 98% of the rock consists of quartz and feldspar in graphic intergrowth. ×22.

(the distance by trail across this is nearly ten miles). We have previously referred to the presence of rhyolite in the midst of this granite (samples Nos. 7a and 7c). The presence of this granitic mass between the two sedimentary areas is peculiar but we do not know what relations exist between the granite and the sediments.

The sample of granite from the Río Pastaza was collected between the hut called Cashaurcu and a ridge called Abitagua about three miles west of Mera on the north bank of the Río Pastaza. The rock is strikingly graphic in a very coarsely microscopic way, the grains ranging from one to two

millimeters in dimensions. Quartz and alkali feldspar compose over 98%
of the specimen. The feldspar consists chiefly of orthoclase, cryptoper-
thite, and very little oligoclase-albite. It is all turbid from slight kao-
linization, and the quartz is crowded with liquid and gas inclusions.
A few little magnetite crystals and tiny zircons represent the minor acces-
sory components, and an occasional microscopic fracture is filled with
epidote. In addition to slight kaolinization many of the feldspars are very
sparingly flecked with fine scaly sericite and minute random patches of
zoisite-epidote, but on the whole the rock, a typical graphic granite, is
comparatively fresh.   Figure 24 illustrates the general character of this
specimen.

Río Urcusikiyacu

Specimen a.   The trail from the Guacamayos Ridge south toward the
Río Napo crosses an area of granite lying between the base of the ridge
and the Río Jandache, where the presence of altered volcanics beneath the
Albian sediments which bound the south wall of the valley of the Río
Jandache has previously been referred to.   The sample was collected
from the trail on the right bank of the Río Urcusikiyacu, 3.33 miles north
of the Río Jandache at an elevation of 4,630 feet above the sea.   The
specimen of granite collected in this locality is a coarse textured, very
inequigranular, light colored rock composed of quartz, albite, microper-
thite, microcline-microperthite, and a little biotite.   The feldspars and
the biotite show only incipient alteration, and there is a slight development
of limonite in minute hair-fractures in the rock.   There is some evidence
that the perthitic feldspars originated through partial replacement of
earlier orthoclase by end-stage albite; this is shown by the extremely
ragged unoriented albite streaks in the orthoclase that cut across the
cleavages, and by the interstitial and marginal distribution of albite and
quartz that have effected some marginal replacement of the earlier feld-
spar.   The rock is a simple biotite granite.

Río Napo

Specimen b.   A very peculiar occurrence of granite was observed on the
Río Napo, about five miles below the pueblo of Napo.   On the left bank
of the river at a place called "Remolino de Latas," nearly horizontal
limestones of Turonian age were seen.   On a hill about one hundred
feet above the surface of the river, we encountered several boulders some
six feet in diameter, lying on the limestones.   We are ignorant of both
the source and the origin of the granite boulders.   They have the ap-

pearance of boulders transported either by glaciers or flows of lava; they may possibly represent an inlier of granite, but this is very doubtful.

The sample is a simple biotite granite that differs from the granite on the Urcusikiyacu river only in minor internal structural details, and in the degree of alteration of the feldspars. The component grains are extremely irregular in outline, with strongly interlocking margins. The interlocking of the quartz and feldspar develops into micrographic structures in places, and there is a tendency toward the production of protoclastic structures on the margins of occasional grains. The feldspars are in large part microperthite and orthoclase, with a smaller amount of oligoclase. The orthoclase and microperthite are very turbid, owing to the formation of opaque-white kaolin mixed with a little sericite and minute grains of zoisite-epidote. Some of the biotite present has been altered in part to chlorite. Occasional random grains of magnetite and a few minute grains of zircon form the only accessories.

(d) QUATERNARY LAVAS

All the metamorphic and igneous rocks described in the preceding pages refer to rocks judged to be pre-Andean in age. They were probably metamorphosed and extensively altered before the uplift of the Andes, which we now believe took place in very late Tertiary time.

The lavas which were extruded and the ash which was cast forth over the surface during the formation of the Andes, and up to the present day, is characterized by freedom from alteration. The component minerals are always perfectly fresh. Where one can examine the lava streams which are still uneroded, it is possible to recognize these lavas without petrographic study.

We have previously referred to the lavas of the volcano Sumaco which, during the opening of the orifice in the Cretaceous sediments and during the activity of the volcano, were poured forth on the surrounding Cretaceous rocks. The lavas of Sumaco have been described (1), but so far, unfortunately, no one has been able to collect any samples of the lavas of the volcano "El Reventador," which came into activity in 1926 on the Río Coca.

Apart from these two centers of volcanic activity in what has been considered a region separate from the Andes, it is probable that other Quaternary and recent lavas have been poured out on the surface in other localities not yet discovered. In 1921 we noted blocks of fresh lava in several places on the sediments; on the Río Misahualli, again on the divide between the Río Anzu and Río Puyo at about 4,000 feet elevation, and also on the Río Ila a few miles above the pueblo of Napo.

The samples herewith described may represent the lower parts of recent lava flows from the volcano Antisana.

Sample No. 10 was collected on the trail from Papallacta to Baeza, at a point 16.3 miles east of Papallacta and at an elevation of 6,290 feet above the sea. It is a very dark gray, slightly porphyritic, vesicular rock, somewhat rusty through weathering. The groundmass is composed of tiny microlites of fresh basic plagioclase crudely oriented in a flow structure and distributed in a mesostasis of dark altered glass which is filled with multitudes of specks of iron oxide. In addition there are granules of partially altered olivine, granules of augite, and little crystals of magnetite. Scattered through the groundmass there are somewhat larger, but not phenocrystic, crystals of labradorite, olivine and augite. The rock also carries phenocrysts of clear, zoned labradorite, commonly badly corroded and filled with groundmass matter that is distributed both zonally and heterogeneously in the feldspar; and crystals of augite, some euhedral, others exhibiting corrosion, with the development of almost colorless and more brilliantly polarizing margins quite distinct from the main part of the crystals. The augite is faintly pleochroic grayish-green to faint rose-pink, optically positive, $Z_\wedge c = 38° - 10°$, and has distinct dispersion. The rock is a basalt, unaffected by dynamic movements and but very slightly affected by weathering. It is certainly much younger than the schist, and perhaps younger than the silicified and kaolinized andesite No. 2-b that occurs in the vicinity of Papallacta. This, however, is purely conjectural. It is probably lava from one of the neighboring volcanoes.

Specimen 2 represents an occurrence near Chalmayaca, 9,000 feet south of the end of the Baeza Road. It is very dark gray, fine textured and porphyritic, with "chalky" looking phenocrysts.

The groundmass is hyalocrystalline, filled with many tiny microlites of plagioclase arranged in flowage structure, and containing irregular patches of a clear, low index substance that consists of tridymite, occurring in characteristic "spearhead" or "wedge" twins. The phenocrysts are crystal clear plagioclase and wholly altered hornblende and biotite. The plagioclase is poorly twinned but very strongly zoned; the zoning is so prominent and the change in composition so continuous that the plagioclase phenocrysts do not completely extinguish in any position.

Judging from their indices of refraction, considerably higher than balsam, and approximate extinctions (complete extinction is not found) measured from cleavages, the feldspar phenocrysts have an average composition corresponding to a basic andesine. They are veined with an

isotropic substance whose index of refraction is considerably lower than 1.535, resembling analcite (?), clear and colorless in transmitted light, but somewhat opalescent by reflected light.

The phenocrysts of hornblende and biotite have been completely converted into fine mixed aggregates of magnetite and hematite. A little magnetite in euhedral grains, a few small crystals of fresh augite, and occasional turbid crystals of apatite, constitute the accessory minerals.

The rock has not been subjected to any deforming stresses at all; it is a simple andesite with a simple history, much younger than the schists, and possibly related in time and origin to the basalt No. 10.

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COMPARATIVE PHYSIOLOGY OF THE GASTRIC HUNGER MECHANISM *

By THOMAS L. PATTERSON

CONTENTS

INTRODUCTION

Before men and other animals had progressed to the point of having minds, so that they could feel hunger, pain, fear, rage and other types of emotional excitement, the organism was merely a community of living cells. Yet this community must have had some way of meeting danger from without; otherwise it would never have survived to develop into the animal and human bodies we know today. In other words, before conscious mind evolved there was the automatic protective response of the living thing which still operates today in the unhappy physiological "kicks" produced by various types of external stimuli playing on the organism. These primitive experiences are not peculiar to man alone but are shared with the lower animals. A knowledge of the conditions accompanying these experiences is, therefore, of general and fundamental importance in the proper interpretation of animal behavior and of the social life of human individuals.

One of the most fundamental of all the phenomena which characterize animal life is the spontaneous motility of the animal organism. This animal activity, although it varies widely in form and extent from species to species, is an ordinary phenomenon which one always anticipates under normal physiological circumstances. We may ask, then, what is it that marks the diverse performances which animals display? Their activity is ordinarily considered to be the result of some form of external stimulation. Yet all animals, from the lowest unicellular organism to man, are active even when all external stimuli have been eliminated. This spontaneous motility, just like the motility of the gastro-intestinal tube and other forms of bodily activity, must have a definite cause, the underlying physiological origin being due to some natural factor within the organism itself. In brief, the biological requirements and behavioristic reactions of all animals in the zoological scale, including man, are to a large degree governed by "internal drives" of the cell mechanism; the hunger urge is only one of many such existing factors leading to alterations in the bodily economy.

Carefully conducted experiments of a comparative nature on the movements of the empty stomach of numerous vertebrate and invertebrate animals have made it possible to increase materially our knowledge of the functional mechanism of this very important organ, to unravel hidden secrets which previously we did not know existed, and to explain them in more or less understandable terms of physiology.

Since the alimentary tube is an enfolded portion of the body surface, food taken into it is not in the body but is merely enclosed. Therefore, in virtue of the circular and longitudinal muscular layers contained within its walls, it is a contractile tube, capable under normal conditions of performing peristaltic and segmental activity which is so essential in the

proper transportation and disintegration of the ingested food. At the same time, by means of its epithelial lining and digestive glands (including the accessory glands of digestion) it is a digestive tube for making soluble, through enzymatic action, the food material, in order to meet the nutritional needs of the tissue cells of the body. In other words, the tube is so constructed anatomically, and so controlled by nerves, that it can easily perform those mechanical and chemical processes governing food digestion.

However, when the stomach is in the empty or nearly empty state it may also exhibit active peristaltic movements giving rise, at least in man and the higher animals, to the complex sensation called hunger which urges, drives and compels man and animals to the ingestion of food. In the persistence of hunger it is a sensation so disagreeable, so tormenting, that men have committed crimes in order to assuage it. It has led to cannibalism, even among the civilized. It has resulted in suicide. It has defeated armies. And it has led to the mutiny of sailors on shipboard— for the aggressive spirit detaches itself from loyalties and becomes personal and selfish as the hunger pangs increase in vigor and insistence.

It has been shown in gastric studies on man and the higher animals that analogies as well as differences between the activity of the stomachs of these animals exist, but very little research, as yet, has dealt with the complete analysis of the hunger mechanism in the lower vertebrates and no papers have appeared which deal with the graphic analysis of this problem as related to that great group of invertebrate animals. It is generally conceded that environmental changes in climate, temperature, and food, over extended periods of time, are more or less reflected by changes in the gastro-intestinal canal. By studying these correlated data one should be able to explain some of the underlying causes of these structural and functional variations and thereby be aided in a more complete interpretation of the complex mechanism of the stomach of man.

The writer has selected those animals from the phyla of the vertebrate and invertebrate groups—including terrestrial and marine forms that lead lives of very diverse character—which could be modified through surgical procedures to meet best the technique required for such an experimental investigation. They are, thus, suitable subjects for investigations concerning variations in the functional relationships of the gastric mechanism. It is the purpose of the present paper to attempt a more or less comprehensive analysis of the hunger problem as related physiologically to the series of diverse animals selected for this investigation. Such a study is not only of value to biology, to comparative physiology, to experimental and clinical medicine, but it also has its economic importance.

THE BIOLOGICAL SIGNIFICANCE OF HUNGER

HUNGER IN THE PROTOZOA

Biologically, hunger is a condition that leads to the taking of food and it may be considered more fundamental or primitive than the urge of sex, since bodily nutrition is a necessity in all forms of life. The underlying mechanisms in the genesis of the hunger urge in the higher animals is obviously a sensation involving a more or less complex nervous organization. Therefore, hunger as a sensation or conscious process is probably confined to such animals as possess a nervous system and an alimentary canal, aided possibly by a humoral mechanism. What, then, are the factors that lead to the ingestion of food in the unicellular and in the simpler metazoic animals which have no specialized nervous system? Are the primordial factors that cause an amœba to pursue and engulf another unicellular organism comparable in any way to the mechanism of the hunger urge in man and the higher animals?

All the unicellular organisms, including the simpler parasitic forms, live, at least during their periods of activity, either in water, in animal or plant fluids, or within the living cells of other animals. Under these conditions the food materials are in solution in the medium surrounding the cell or the animal and the process of feeding is essentially the same as that of the tissue cells composing the bodies of higher animals. According to Pütter (190),[1] this may apply to all the lower forms of life inhabiting the waters of the earth. We know that all metazoa feed on other unicellular animals and plants, whole or in fragments, and that they are taken into their bodies as food, and digested. The processes of ingestion, digestion and egestion, in a simple form like the amœba, may be said to be accomplished through the super-mechanical properties of the living protoplasm composing its body. In brief, it is a property of the protoplasm to develop temporary organs to meet the needs of the organism. When food is ingested a temporary mouth is formed by the engulfing process and as the food particle enters the body of the organism some water is taken in with it, and a food vacuole is formed that functions as a temporary stomach. It is assumed that the food substance is then made soluble through the action of a digestive enzyme or enzymes present in the cell fluid which, finding its way through the membrane of the food vacuole, attacks the food. Any non-digestible portion is expelled through a tem-

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[1] Throughout the present paper the numbers in italics enclosed by parentheses refer to works similarly designated in the bibliography.

porary anal opening or vacuole of egestion. The ingestion of solid particles by this primitive amœboid organism is practically identical with that found in the special phagocytic cell in the higher animals, although the latter is probably not primarily a feeding apparatus.

In many protozoan organisms the active feeding stage appears to be almost as continuous as contact with food particles permits. A few of these organisms seem to be able to differentiate between nutrient and non-nutrient particles while others take them up more or less indiscriminately. Jennings (*104*) in his studies of the feeding processes of amœba, reports that the animal may remain at rest for a few minutes following the ingestion of food; but since the amœba becomes active again before the food is actually digested, the brief rest period cannot be interpreted as a state of satiety. According to Verworn (*231*), the phenomena of feeding, in the protozoa, including a certain capacity of selection of food, involve automatic motility initiated through chemo- and stereotropisms only, but no statement is made as to whether the rate of this motility varies with the degree of hunger. Hodge and Aikens (*93*), working on the vorticella, found that the cilia worked uniformly and continuously night and day, in drawing in and assorting food particles. But the authors were unable in any appreciable degree to satisfy the apparent hunger of these animals by an abundant food supply. In paramecium, an extensive food supply leads to a decrease in the activity of the body cilia. The animal comes to rest, but the oral cilia continue to draw food particles into the mouth at approximately a constant rate (*103*). Wallengren (*236*), on the contrary, observed no changes in ciliary movements and vacuole contractions or in the excitability of this animal during hunger except for a decreased activity when the paramecium was near death from starvation. However, Schaeffer (*208*) has described in *stentor* certain differences in behavior between the states of hunger and satiety. When the animal is gorged with food it remains somewhat contracted, the activity of the membranellæ are markedly decreased, it is less excitable to external stimuli, and it discriminated more carefully between food particles and indigestible particles in the water current. It is evident that a state of depletion or hunger in *stentor* leads to increased excitability, increased motility, and increased avidity of food ingestion. It is possible that future investigations will reveal similar differences in most of the unicellular animals. Therefore, can this increased activity in a protozoan like *stentor* be considered as expressions of conscious states, analogous to the hunger urge in higher animals?

HUNGER IN THE SIMPLER METAZOA

The mechanism of phagocytosis in the metazoa is not primarily a feeding process, but it is concerned with the destruction of cellular debris and cells foreign to the organism. Furthermore, the metazoan phagocytes probably feed on the organic substances in solution in the body fluids as do the cells of other tissues. It is possible that the rate and quantity of ingestion of the foreign cells may depend, in part, not on the condition of the phagocyte, but on certain substances—of an opsonic nature, present in the body fluids—that act in a sensitizing manner on these foreign cells, thus augmenting the process of phagocytosis. Such a process is not known to exist in the feeding phagocytosis of the protozoa, but it does not necessarily imply that the essential mechanics of the phagocytic processes in the two groups are different.

In actinians, both ciliary and muscular activity are involved in the appropriation of food. Chief among these are the response of the oral cilia and the movements of the tentacles, both of which are open to significant changes of the utmost importance in judging of the relation of this process to the animal as a whole. Unlike the tentacular cilia, the oral cilia, those of the lips, and of the esophagus, may reverse the direction of their stroke, thus converting the usual outward current into an inward one. Under ordinary circumstances the reversal of the oral cilia is accomplished by dissolved substances from the food and in the earlier studies made by Parker (*163*) on the sea anemone (*Metridium*) it was believed to be the only way by which such a reversal could be induced. Later, Torrey (*226*) showed that such a reversal could be brought about in *Sagartia* by mechanical stimuli as well as by chemical means and that it was favored by a starved condition of the animal. Allabach (*3*) also found that such a ciliary reversal could be induced in *Metridium* by mechanical stimulation and Gee (*83*), using specimens of *Cribrina*, found that those kept in the laboratory for some time failed to give a reversal to mechanical stimuli, whereas such animals in their native pools gave evidence of it. Allabach (*3*) also found that in *Metridium marginatum* some individuals, on mechanical stimulation, readily reverse their ciliary stroke, others less readily, and still others not at all; these variations are dependent upon whether the animals have been starved or fed. For example, in two underfed specimens there was a reversal of cilia to clean filter-paper, and then, when they had been vigorously overfed and the filter-paper test repeated again after three hours, there was total failure of any reversal of the cilia and the paper was consequently re-

jected. In another test, made eighteen hours after the feeding, the paper was engulfed, showing that the cilia had returned to the state characteristic of animals that lacked food. It is therefore evident that an underfed *Metridium* will reverse the effective stroke of its oral cilia to mechanical stimulation, while a small quantity of food will abolish this peculiarity and leave these organs incapable of such reversal.

However, will meat or meat extract induce this reversal after the anemone is gorged with meat or other forms of food? This investigator concluded that the loss of power to reverse the stroke of the oral cilia was the result of the difference in metabolism between a well-fed and an underfed individual.

In a further analysis of this explanation, it was found that when the esophageal tubes of *Metridium* were cut from recently fed animals and experimented with as ciliated membranes, they exhibited well-marked ciliary reversal to pieces of clean filter-paper, while to fragments of mussel they reversed the ciliary stroke in the way characteristic for food; but after a dozen or more such trials they were no longer able to show this reversal. This loss of the reversal of the ciliary stroke Allabach (*3*) believes is referable to a factor of fatigue since the mechanism of the animal in the undisturbed state is at its greatest sensitiveness. On feeding, however, its efficiency diminishes so that filter-paper no longer excites a reversal, a change which is now called forth only by the more vigorous stimulation from the dissolved products of the food.

The feeding movements of the tentacles in actinians are obvious neuromuscular reactions, as is proven by their disappearance on narcotization with chloretone. It has been found that these responses gradually became slower or even ceased as feeding progressed in both *Metridium* and *Cribrina*. Jennings (*105*) has applied crab meat to the left tentacles of *Aiptasia* and observed a quick transfer of the food particles to the mouth, but after five such tentacular reactions they quickly diminished and ceased. The right tentacles responded in a similar manner when stimulated, after which the left tentacles could again be induced to respond sluggishly for a few times. On the contrary, Allabach (*3*) with *Metridium* and Gee (*83*) with *Cribrina* obtained only negative results. It is the opinion of these last two investigators that the change in the tentacular responses after continuous feeding is due to sensory fatigue and not to a general metabolic condition, although they admit that the food substances unquestionably serve as material for metabolism and eventually must influence the general state of the animal. The seat of the modified responsiveness lies very largely in the individual tentacles and is consistent

with the structural organization of the animal and the nature of the nerve-net, thus emphasizing the relative independence of parts rather than the action of the organism as a whole (*164*). Therefore, in the actinians there exists a state of hunger whose complexity is in proportion to the neuro-muscular development of the animal.

As regards investigations on the hunger mechanism, little or no work of importance has been found on representatives from the following phyla—namely, Porifera, Echinodermata and Annulata.

HUNGER IN PLANTS

The general biological conception of hunger is probably as applicable to the lowest, or unicellular, plants, as to the unicellular animals. There are numerous studies on the chemotactic and general tropic behavior of the lower plants (*186, 113, 115, 212*), but an examination of the literature reveals nothing as having any direct bearing on this subject. Kniep (*113*) believes that bacteria are endowed with the senses of taste and smell and he has shown that they respond to certain chemical stimuli which are dependent upon the reaction of the culture medium. However, no attempt was made to determine the effect of the quantity and nature of the food in the culture medium on the response of these bacteria. Neither did Kendall and his students (*110*) in their extensive studies on the metabolism of bacteria consider the effect of starvation on their behavior.

It is probable that the swarm cells of spore-bearing plants feed by phagocytosis in the same manner as the unicellular animals and that the factor of hunger similarly urges both the plant and animal organism to the ingestion of food. According to Lister (*120*) the swarm cells of mycetozoa are quiescent for an hour or more after the ingestion of micro-spores and bacteria. Most plant organisms, however, feed primarily on the inorganic material in the soil and on the carbon dioxide of the air, but a few, like certain of the bacteria, the swarm cells of the sporophytes, the parasitic plants, and to a certain extent the so-called carnivorous plants, demand organic material.

Blanchan (*16*) states that "the animalcule and the insectivorous plant know no boundaries between the animal and the vegetable." In other words, animated plants and vegetating animals may be said to parallel each other. In the pitcher-plant the petiole is modified into a deep hollow pitcher while a modification of the blade of the leaf forms its spout. The pitchers are usually half filled with fluid consisting of water and secreted juice. A sweet secretion within the pitcher's rim invites flies and other

small insects to enter; on the Pacific Coast the golden jars of *Darlingtonia californica*, with their overarching hoods, are often so large and watery as to drown small birds and field mice. The victims soon find their escape cut off, become exhausted and sink into a watery grave. The organic products of their bodies' decay are then absorbed by the plant as nourishment in the form of soup. The sundew is another characteristic plant of the carnivorous group which actually masticate their animal food, thus depending upon it to meet their nutritional requirements. A small fly or gnat alights on one of the reddish dew-covered leaves only to find that the clear drops instantly glue its feet. The reddish leaf hairs, acting like tentacles, imprison the struggling victim as the sensitive hairs are excited. As more of the sticky fluid is excreted it covers the legs, wings and the tracheal pores on the body, through which the insect breathes. The curved leaf rolls inward, thus forming a temporary stomach, while the hairs bind and the glue suffocates the victim. The food is now digested by a freshly secreted peptic fluid of a complex nature, the chemical analysis of which shows that it is practically identical with the gastric juice of the human stomach. Darwin fed these leaves with various substances and found that they were able to digest pollen, seeds, grass, etc., whereas bits of undesirable substances, like chalk or wood, were rejected. He also poisoned these plants with acids, and gave them fatal attacks of indigestion by overfeeding them with bits of raw beef. This is an instance of a remarkable degree of specialization and adaptation, for in certain plants, like the above, which grow in peat bogs whose soil is deficient in nitrogen compounds, there is an interference with the normal protein formation and they then come to depend more or less on a carnivorous diet. This would indicate that there actually existed in this plant a condition of protein hunger which in a way might be considered more or less comparable to the salt hunger in animals that have been known to travel great distances in search of salt "licks". In the feeding processes of higher plants, motility, apart from growth, plays only a minor rôle for there is no visible evidence that starvation increases excitability and motility as in the lower plant organisms, which is probably necessary in order to induce a biological state of hunger.

Hunger in the Higher Animals

The complex sensation that urges man and the higher animals to the ingestion of food is called hunger and appetite. These two sensations are very intimately interrelated and a clear understanding of these two terms is necessary before proceeding. According to one view, appetite is the first

degree of hunger. It is associated with a desire to eat and is mild, pleasant and agreeable in character. Hunger, on the contrary, which is the result of not satisfying appetite, is a more advanced condition, disagreeable, unpleasant and even painful. From this viewpoint appetite and hunger would differ only quantitatively.

The more acceptable view holds that appetite is related to previous sensations of taste, smell and appearance of food. There are important psychical elements concerned in its composition. Thus, through associated memory and experience one is able to anticipate the odor and taste of a delicious beefsteak, sensations which are followed by the characteristic reflex salivary watering of the mouth. Hence, appetite and hunger are widely different sensations, both as to physiological basis, localization and psychical elements. What guest at the banquet table is still hungry when the tempting dessert is served; and yet, who refuses it on the plea that he no longer needs it? Therefore, hunger may be satisfied while the appetite calls, and vice versa.

Hunger, as experienced by man, is a more or less uncomfortable feeling of tension or pressure—of the nature of a dull ache—referred to the region of the stomach or epigastrium. This is usually the organism's first demand for food, and if it is not obeyed, the sensation ordinarily grows into a highly uncomfortable pang or gnawing feeling of "emptiness." The cry of the new-born child for food is, in all probability, the result of this pure hunger pang plus the inherited "desire for food," while the quieting effect of feeding is due to its abolition. It is a sensation exhibiting varying degrees of pain and is the one indispensable element in hunger. It is often accompanied by accessory phenomena the most common of which is a feeling of general lassitude or weakness. Headache, nausea, nervous irritability, vasomotor instability, and even fainting, may appear as part of the hunger complex.

The genesis of the hunger pangs may be found in certain contractions and tonus states in the stomach, the afferent nervous impulses thus initiated affecting certain parts of the brain. Therefore, the hunger mechanism in man requires a nervous system, a muscular digestive tube, and afferent and efferent pathways connecting the two. Such anatomical conditions are common to all vertebrates and to the various invertebrate groups down to and including the cœlenterates.

Another characteristic factor in the hunger urge as it exists in man and the higher animals is its periodicity or intermittency. This is true until we reach the amphibian group of animals in which the gastric hunger activity becomes continuous. There are also other animals like the turtle

which exhibit a modified periodicity. The details bearing on such variations in the hunger motility of the stomachs of these animals will be discussed in the following sections of this paper. In general, the influence of the hunger state on the behavior is essentially the same in each of them. There is increased nervous excitability and restlessness, but the restlessness is probably not primarily the result of the consciousness of the hunger feeling, since it is in evidence in dogs and birds that have been decerebrated. In starving animals, strong hunger apparently inhibits fear since they become more bold and ferocious; in man, similar hunger states tend to produce a contentious and unsocial disposition.

The empty or nearly empty stomach is a requisite for the onset of the hunger sensation in man and probably in the carnivorous animals. However, this is not the case in the ruminating animals and in the herbivora in general, the stomachs of these animals not being empty even after days of starvation. The feeding in birds is also more or less continuous, even when the crop or gizzard is filled with considerable food. These animals either do not feel hunger on a partially filled stomach, or else they eat because of appetite in the absence of the hunger urge.

There is considerable experimental evidence that the intensity or persistence of the hunger urge parallels the degree of activity and the rate of metabolism in the normal animal. Therefore, hunger is more intensified in the young and growing than in the aged and inactive animal. In warm-blooded animals hunger is augmented by external cold and depressed by external heat, whereas just the reverse is true in the cold-blooded animals (frog).

The Theories of Hunger

The theories advanced to explain the genesis of hunger and appetite may be said to fall into three main groups, namely: 1. Those of a *peripheral origin*, involving the stimulation of sensory nerves chiefly in the digestive tract. 2. Those of a *central origin*, involving a direct stimulation of a hypothetical "hunger center" in the brain by the blood or by changes in the metabolism in the center itself. 3. Those of a *general sensation*, involving a combination of both central and general peripheral factors of hunger. For a detailed account of the ancient and modern theories of hunger the reader is referred to the extensive studies by Cannon (*35*) and Carlson (*47*) of man. The generally accepted modern theory of the cause of hunger is the stimulation of sensory nerves in the wall of the stomach (muscularis or submucosa), especially in the fundus and cardiac regions,

by contraction of the empty or partly empty stomach. This view will form the basis of the discussion in the following sections of this paper in connection with the results obtained from representatives of the various animal groups investigated.

METHODS OF EXPERIMENTATION

Several methods may be employed for studying the tonus and contractions of the empty stomach, both in man and experimental animals, namely: (1) direct inspection by means of a permanent opening or gastric fistula into the stomach through the abdominal wall; (2) the introduction of a delicate rubber balloon into the stomach, either via the esophagus or through a gastric fistula, and recording the variations in pressure on the distended balloon, caused by the contractions of the stomach; (3) the introduction into the stomach of a double walled rubber balloon with a layer of bismuth paste between. This permits graphic registration of the stomach movements synchronously with X-ray photography or inspection by means of the fluoroscope. In the various animals used in this investigation all three methods have been employed. The necessary alterations in technique in order to meet the anatomical peculiarities of the animals studied will be discussed under the sectional heads.

COMPARATIVE PHYSIOLOGY OF GASTRIC MOTILITY IN VERTEBRATE AND INVERTEBRATE ANIMALS

There is practically nothing in the literature on the movements of the intact empty stomach of any of the invertebrates. About fifteen years ago the author began a series of comparative studies on the movements of the empty and filled stomach of some of the lower vertebrate animals with the intention of extending the studies to certain of the invertebrate forms. Much information of theoretical interest can be obtained from comparative studies of the gastro-neuro-muscular mechanism. In brief, the interest of the digestive mechanism of lower forms of animals lies in the fact that digestive problems similar to those confronted by higher forms have been solved in different ways, and these are an important aid in helping to unravel problems of such complexity as those which exist in the primate forms of life (man, monkey, etc.).

As yet, there are insufficient data to show the differences and similarities between the types of gastric activity as represented in the various animal groups, and this is notably true in the case of the invertebrates. The paucity of data in this respect may be appreciated readily by exam-

CLASSIFICATION OF INVERTEBRATE ANIMALS STUDIED

INVERTEBRATA

ARTHROPODA

CRUSTACEA

CRAB
(Cancer
productus)

MOLLUSCA

GASTROPODA

AMPHINEURA

PELECYPODA

ABALONE
(Haliotis
rufescens)

SEA HARE
(Tethys
californica)

GIANT SLUG
(Ariolimax
californicus)

CHITON
(Cryptochiton
stelleri)

GAPER CLAM
(Schizothaerus
nuttallii)

NOTE {1. Animals studied by author, in Roman type.
{2. Animals studied by other investigators, in bold face.
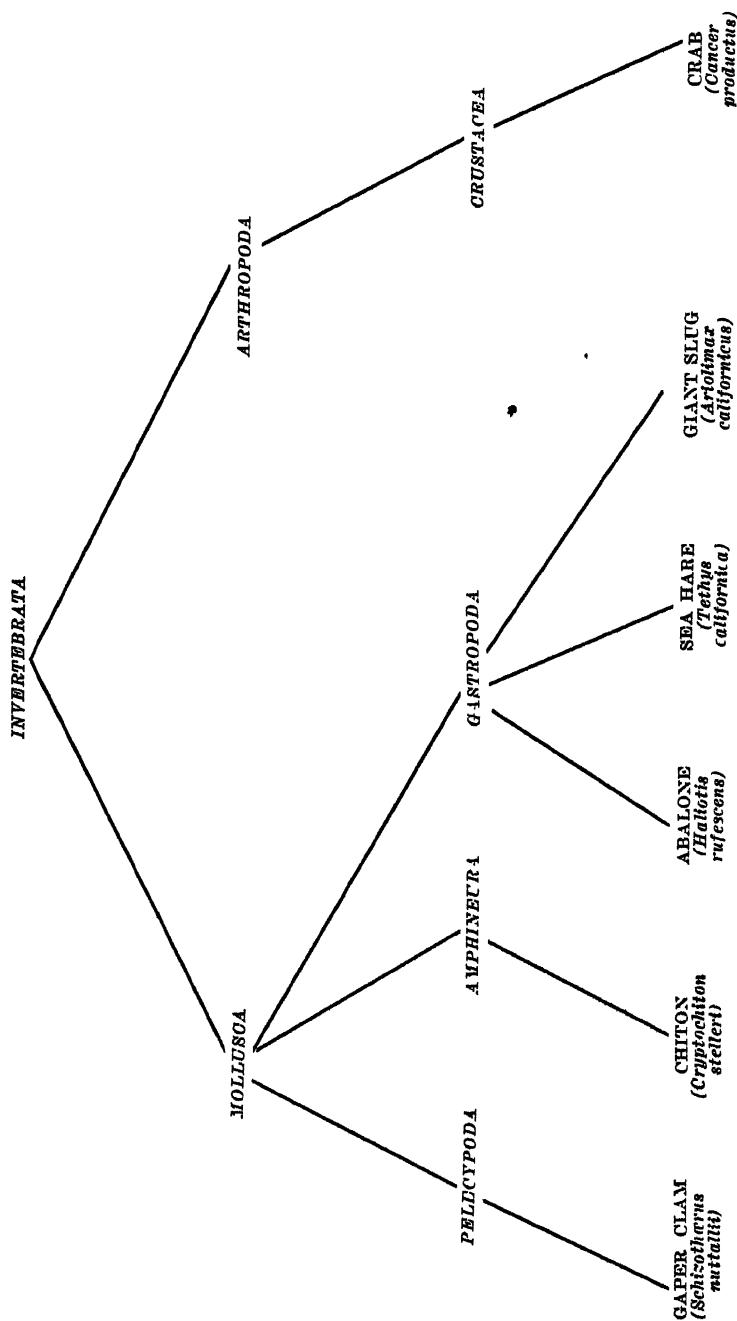
CLASSIFICATION OF VERTEBRATE ANIMALS STUDIED

VERTEBRATA

CHORDATA

CYCLOSTOMES — HAGFISH (*Polistotrema stouti*)

PISCES — DOGFISH (*Squalus californicus*)

AMPHIBIA — NECTURUS (*Necturus maculatus*) — FROG (*Rana catesbiana*)

REPTILIA — * TURTLE (*Chelydra serpentina*)

ATES — * PIGEON (*Columba sp.*)

MAMMALIA — * DOG (*Canis familiaris*) — * MONKEY (*Macacus irus*) (*Macacus rhesus*) (*Cynocephalus anubis*) — * MAN (*Homo sapiens*)

Horse — Ox — Goat — Sheep — Rabbit — Guinea-pig

NOTE { 1, Animals studied by author, in Roman type.
2, Animals studied by other investigators, in bold face.
* Duplication of work.

ining the works of Cannon (*34*) and Carlson (*47*) on the behavior and control of the gastro-intestinal tract.

The animals of these two great divisions (Vertebrata and Invertebrata) so far studied have been classified on the following pages.[2] The Roman type on the charts (pp. 70-71) indicates animals studied by the author; bold-face type, animals studied by other investigators. It will be observed further, that all classes (Mammalia, Aves, Reptilia, Amphibia, Pisces and Cyclostomes) of the vertebrata of the phylum Chordata have one or more representatives that have furnished observational material for this investigation. Studies on the phyla of the Invertebrata are incomplete at this writing, only two of the higher phyla of this group having been studied, namely, the Mollusca and the Arthropoda. One or more representatives from each of the three classes of the Mollusca, namely, Pelecypoda, Amphineura and Gastropoda, have been selected as being suitable types for making gastric studies and also a single representative from the class of the Crustacea of the Arthropoda phylum. The gastric activity of the different animal representatives studied will now be considered individually and more or less briefly under the headings of the Vertebrata and the Invertebrata, respectively.

TYPES OF INVERTEBRATA STUDIED

ARTHROPODA

CRUSTACEA

CRAB (*Cancer productus*)

The question of the rhythmical spontaneous movements of different parts of the alimentary canal of vertebrates now occupies an extended literature, but only a few parallel observations on the organ in a state of repletion have been made on the invertebrates. Ten Cate (*221, 223*) has contributed work on the isolated terminal intestine of *Astacus*, the European fresh water crab (crayfish) and the esophagus of a diving beetle, *Dytiscus marginalis*. The isolated specimens were suspended in aërated Ringer's solution and attached to a lever for the purpose of recording the spontaneous movements. These experiments demonstrated that the isolated terminal intestine of the crayfish, as well as the isolated esophagus of the diving beetle, can exhibit under favorable circumstances automatic

movements which possess a more or less rhythmical character and show at times feeble fluctuations of tonus. Furthermore, the esophogeal preparation of the diving beetle manifests for a long time automatic movements which exhibit a rhythmical character and are superimposed on the oscillations of tonus. These automatic movements are influenced by drugs which provoke changes in the tonus as well as in the amplitude and the frequency of the pendular movements. Carlson (48) has also reported that the alkaloids, curare, atropine, and nicotine, stimulate and paralyze the central nervous system, peripheral (visceral) ganglia, and the denervated heart in mollusks and arthropods. However, these substances do not paralyze the motor nerve endings to the skeletal or the visceral muscle but they do paralyze the cardio-inhibitory nerves without affecting the cardio-accelerator fibers.

Hardy and McDougall (90) working on small fresh water crustaceans, *Daphnies,* have described rhythmical peristaltic movements in the intestine which starts from the anal region and propagate themselves up to the small intestine. They are of the opinion that these rhythmical movements are produced independently of the central nervous system. They have also observed these movements on the isolated intestine.

In the work on the visceral nervous system of decapod crustacea, Bottazzi (19) has reported rythmical movements in the terminal section of the intestine of the sea crawfishes, *Palinurus* and *Maja.* According to this investigator the alimentary canal of these crustacea possesses independent motor rhythm which is probably of myogenic nature. Alexandrowicz (2) in a study of the sympathetic nervous system of crustacea, using the isolated intestine of *Astacus* from the masticating stomach to the anal orifice, found that when this was placed in an oxygenated Ringer's solution the rhythmical contractions would continue for thirty-six hours. This author came to the conclusion, contrary to the opinion of Bottazzi (19), that these rhythmical movements of the intestine were of neurogenic origin.

The studies of Miller (147) on the crayfish, *Cambarus,* and on the lobster, *Homarus,* indicate that the intestinal musculature of the anal region, in the absence of a true sphincter muscle, consists of arched and radial fibers supplied by nerves issuing from the last abdominal ganglion. Electrical and mechanical stimulation of the nerve cord or of the intestinal nerves evoke peristalsis in the intestine, and rhythmical opening and closing movements of the anus. It is thought that the coordination existing between peristalsis and anal opening is effected through a local nervous mechanism.

Fig 1 —Ventral aspect
of crab, showing introduc-
tion of balloon via mouth.

THE MOVEMENTS OF THE EMPTY STOMACH AND THEIR INHIBITION

The literature cited gives a comprehensive review of the work published on the activity of the gastro-intestinal tract of crustacea when in a state of repletion, but practically no such observations have been made on this group of animals during the period of fasting.

Comparative studies in the physiology of the gastric hunger mechanism (*180, 181*) have been extended to the crustacea. The large crab (*Cancer productus*) of the Pacific Coast was employed and the investigation was conducted at the new Jacques Loeb Laboratory of the Hopkins Marine Station of Stanford University. During the experimentation the animals were kept in a large vivarium provided with running sea water which was aërated. The stomach balloon for recording the gastric movements was introduced through the mouth (Fig. 1) by pushing back the valvular fold covering the opening into the esophagus at the base of the mandibles after the chelæ had been wedged (Fig. 2). Later it was found advisable to amputate the endognathal palps arising from the meropodites of the third pair of maxillipeds, since the animal ordinarily learns to use these appendages to advantage in working the balloon out of the stomach. The contractions of the gastric mill are periodic, the periods increasing in activity and length until in extreme fasting they become almost continuous on an elevated tonus (Fig. 3 A, C and D).

The gastric activity is somewhat similar to that found in the pigeon and the active periods range from five to twenty minutes depending on the length of the fast. However, the stomach of the crab may sometimes ex-

hibit continuous activity for several hours (Fig. 3 B) but eventually periodicity develops. Sudden inflation of the balloon with air, or increasing the balloon pressure, causes one or more strong contractions. In the earlier stages of fasting there is a marked increase in the gastric tonus during the period of activity which terminates in a fall. The individual

FIG. 2.—The crab ready for gastric registration, dorsal aspect with chelæ wedged.

contractions of the gastric mill are rapid, with practically no intervening periods of rest, while the small and rapid oscillations seen in the curves are caused by the action of the balers. These are the terminal appendages of the exopodites of the various pairs of mouth parts by whose vibratory motion water is kept flowing over the gills. The introduction of small quantities of weak alkali or acid into the water near the animal, as well as body movements, produced temporary inhibition of the gastric contractions (Fig. 4 F and G). Furthermore, when the animal was in a darkened room and normal hunger contractions were being recorded, if the window shade directly opposite was drawn back and forth quietly and at a moderate rate, thus casting light and dark shadows upon the animal, it resulted in producing a temporary inhibition of the gastric contractions (Fig. 4 E).

THE INFLUENCE OF SECTION OF THE EXTERNAL GASTRIC MUSCLES AND THE CIRCUM-ESOPHAGEAL COMMISSURES

In order to ascertain if the external gastric muscles attached to the interior surface of the carapace were exerting an effect on the movements

of the stomach as registered by the balloon method, the anterior pair of
gastric muscles were cut. The necessary procedure consisted in drilling
an opening (three-sixteenths of an inch in width by one-half of an inch in
length) through the dorsal carapace in the mid-line about one-half inch
from the anterior, superior edge of the shell. Following this exposure,
the muscles were cut and the opening in the shell was sealed with plastine
to prevent bleeding or the entrance of water. Such experiments were
without any effect whatsoever on the gastric motility (Fig. 4 C and D).
Furthermore, the stomach was completely isolated from the cerebral gan-
glion (brain) by section of the circum-esophageal commissures. This was
accomplished by drilling a small opening one-sixteenth of an inch by one-
eighth of an inch through the ventral carapace in the mid-line on a level
with the basal segment of the endognathal palps of the third pair of
maxillipeds. Small curved forceps were used to sever the cerebral com-
missures and the opening in the shell was sealed with plastine as in the
case of section of the anterior gastric muscles. Negative results were
again obtained, thus demonstrating that the motility of the stomach of
this animal is independent of the higher nervous center (Fig. 4 A and B).
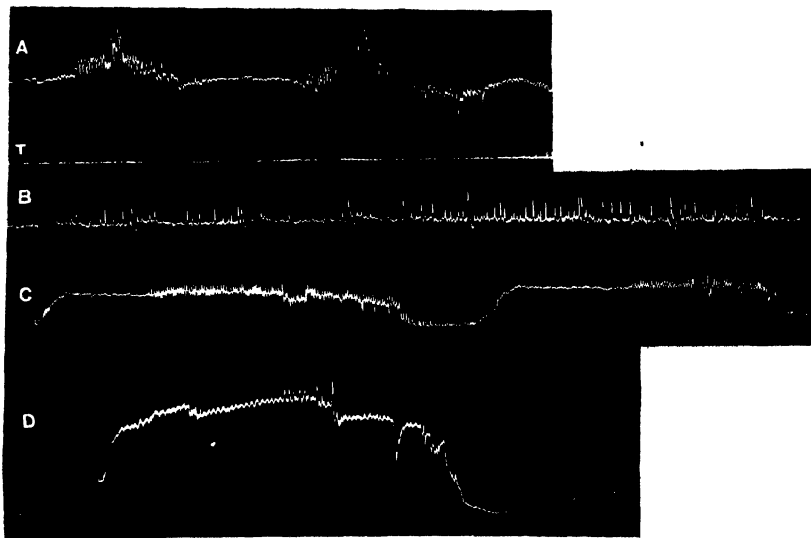
FIG. 3.—A, normal peristalsis, empty stomach of crab (periodic) after a fast of 72
hours. B, continuous hunger activity after a fast of 353 hours, as exhibited in some ani-
mals over a period of several hours. C, periodic hunger contractions on an elevated
tonus after a fast of 379 hours. D, same after section of circum-esophageal commissures,
isolating stomach from central nervous system after a fast of 430½ hours. T, time
intervals in seconds.

It is surprising to note that the tonus and periodic activity of the empty stomach of the crab is more closely related to the gastric hunger activity of the higher vertebrate animals than that exhibited by the stomachs in the forms of molluscs studied. The close similarity existing between the functional activity of the stomach of the crustacean and that of the higher vertebrates would seem to indicate that in the evolutionary development of the stomach, the crab for some unknown reason had stolen a march over the members of the molluscan group.
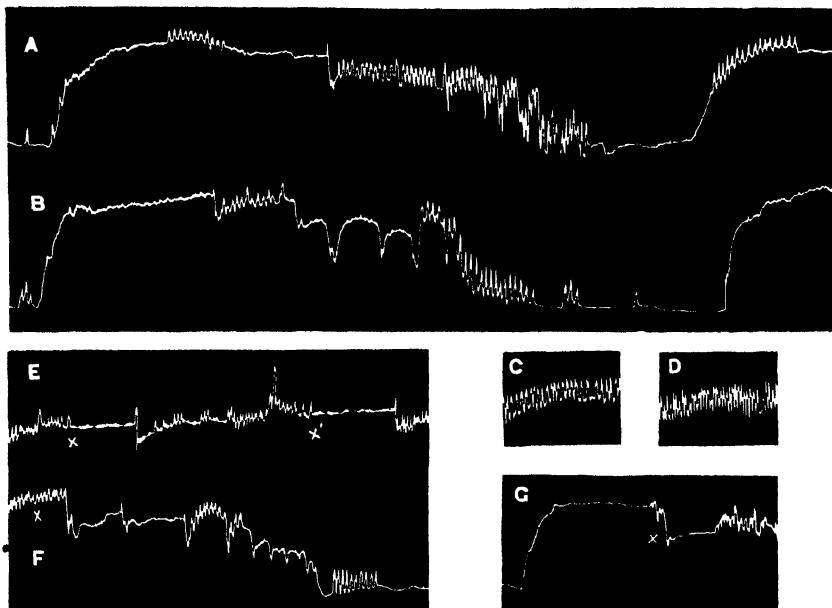
Fig. 4.—A, peristalsis of period of hunger activity after a fast of 412 hours. B, same animal following section of circum esophageal commissures, after a fast of 427 hours, showing complete independence of stomach from central nervous system. C, normal hunger peristalsis after a fast of 200 hours. D, same animal following complete section of anterior gastric muscles after a fast of 209 hours with practically no effect. E, normal hunger peristalsis after a fast of 68 hours, showing reflex inhibition from light at x and x'. F, alkali inhibition from introduction of 10 cc., 1 per cent. sodium carbonate solution, at x, directly in front of animal, after a fast of 411 hours. G, acid inhibition from introduction of 10 cc., 0.5 per cent. hydrochloric acid, at x, directly in front of animal, after a fast of 411 hours.

MOLLUSCA

PELECYPODA

GAPER CLAM (*Schizothærus nuttallii*)

A structure known as the crystalline style appears in a great many molluscs and has attracted the attention of several investigators over the past

years. There has constantly been a question raised as to its exact function. This question has probably been only partially answered, regardless of the fact that many workers have attempted to solve it. That it is responsible in some way for motion of matter in the stomach has been contended by many but usually these contentions have not been based on facts.   .

Nelson (*155*), in his article on the origin, nature, and function of the crystalline style of lamellibranchs, cites the beliefs of certain of the older investigators as to the function of the style as a stirring rod. This investigator has observed the rotation of the style in *Modiolus modiolus,* the ribbed mussel, and in *Venus mercenaria,* the hard clam. He came to the conclusion that the rotary movement of the style is of great importance in separating the food from foreign particles and in serving as a substitute for peristalsis. He was also able actually to observe the style rotating in the stomach, and actually to see food material being separated from sand grains. However, I am unable to find any statement in his article which indicates that he had any just reason for supposing that the action of the style was a substitute for gastric peristalsis.

Edmondson (*74*) found that after the extraction of the crystalline style of *Mya arenaria,* a new style is completely reformed in the proximal portion of the style sac in a period of about seventy-four days, when conditions are most favorable. At the end of the fourth day after extraction of the style, the beginning of a new style may be observed in the style sac. He agrees with Nelson (*155*) that the style rotates in a clockwise fashion and takes the place of intestinal peristalsis.

Rogers (*199*) has summed up the situation in the statement that "a variety of functions has been assigned to the crystalline style. It has been referred to as an organ of support; as an organ in association with the gastric shield, for mastication; as a stirring rod for the stomach contents during digestion; as an aid to absorption either by pressing the alimentary matter against the absorbing epithelium or by acting as a plug to prevent too large particles from entering the intestine and to prevent too rapid movement of alimentary particles; as a reserve of nutriment; as a source of nutriment to useful parasites; as associated in some way with processes of reproduction; as a means of transporting nutriment; as a means of protecting delicate epithelia from abrasion by sand grains, etc.; as a mass of enzymes or enzymes and mucus."

The digestive system of *Schizothærus nuttallii* used in this investigation is, in the main, typical of the Lamellibranchiata, according to Mac-Ginitie (*129*) who has worked upon the species to a considerable extent.

The transverse connections of the dorsal and ventral palps form the upper and lower lips, respectively, of the mouth. There is practically no esophagus, but a relatively large stomach lying just beneath the fused mantle edges in the antero-dorsal portion of the animal.

The crystalline style is located in a style sac which is entirely removed from any connection with the intestine, contrary to the condition found in most clams. The style itself is very large and extends from its sac (the lumen of which it fills almost entirely when complete in size) into the stomach, coming in contact with the opposite wall of the latter organ. The anterior end of the style is very soft, the posterior end tapering and slightly firmer, and the major portion of a particularly firm, gelatinous structure.

The anterior end of the crystalline style works against a so-called gastric shield. The latter structure is made up of chitin and is so arranged that it seems to protect the walls of the stomach from sudden forcible protrusions of the style against the wall. It has lateral processes which probably serve the function of keeping the anterior end of the style within a small area and guiding it while it rotates within that space.

THE MOVEMENTS OF THE EMPTY STOMACH

The gelatinous material of which the style is composed is laid down in a spiral direction indicating that it was so produced by the rotating action of the style itself. That this rotation is brought about by cilia in the walls of the style sac is the opinion of most investigators who have worked on the problem. The intestine is long and greatly coiled.

During the summer of 1928 at the Hopkins Marine Station of Stanford University, Patterson and Boone (*183*) were able to secure a fairly large number of gaper clams, *Schizothœrus nuttallii*. These clams were col-

FIG. 5.—The gaper clam with neck extended, the adult animal measuring in this state 30 inches in length.

lected at low tide in an interesting region known as Elkhorn Slough (*128*). The slough is situated about two miles north of the mouth of the Salinas River in Monterey Bay. When these animals are undisturbed and buried in the mud flats with necks extended so that the apertures of their siphons reach the surface, they may be seen on a quiet, clear day alternatingly spouting jets of water to a height of five or six feet. The clams were transported to the laboratory, some eighteen miles distant, immediately on being dug, and were kept alive in an aquarium aërated by running sea water.

This marine animal is characterized by its long, large siphon, and by the gaping of its valves around the base of the siphon. From this latter characteristic it gets its common name, gaper clam. This is a very large clam, the shell at times attaining a length, antero-posteriorly, of eight or nine inches. When the neck is fully extended in the adult form it measures about thirty inches (Fig. 5). Because of the large size of the animal, the feasibility of introducing a balloon into the stomach, and noting the gastric movements, presented itself. The animal was anesthetized with a solution of one per cent. ether in sea-water, to relax the muscles. Usually a satisfactory anesthetization occupied the greater part of an hour. At the end of this time the valves of the shell were drawn apart from one-half of an inch to one inch, caused, doubtless, by the relaxation of the adductor muscle. The foot was usually extended from the shell, sometimes to the extent of three inches or more. The foot was not inactive, but it could be drawn out of the shell by the experimenter at will. After the animal was anesthetized, the balloon was introduced through the inhalent siphon, passed through the mantle cavity into the mouth and thence into the stomach (Fig. 6). The balloon was then connected by rubber tubing to the recording apparatus and the animal placed in a large vivarium provided with running water.

After recording the contractions by this method for some time, it was found that high peaks appeared in the curve of muscular contractions. On stimulation of the foot or mantles with a glass rod these contractions were recorded by the balloon in the stomach. It was thought, therefore, that some or all of the contractions recorded by the balloon might be caused by the action of the foot or mantle. A check control of this was made by attaching to the anterior edge of the foot a silk thread which passed over pulleys and thence to a light recording lever. This lever was adjusted to write the muscular contractions of the foot directly above the record of gastric contractions so that some comparison might be made between simultaneous actions of the foot and stomach.

THE INFLUENCE OF REMOVAL OF THE CRYSTALLINE STYLE ON GASTRIC MOTILITY

After recording the action of the stomach and of the foot it was decided to extract the crystalline style and record the action of the same two organs in the absence of the style, to determine what effect, if any, the style might have on gastric activity (Fig. 7). The animal was anesthetized as before and a small incision was made in the distal portion of the style sac with a pair of sharp-pointed scissors. The style was removed by means of a pair of blunt-pointed forceps. The style sac extended well into the foot so that its distal end may be readily seen as a small clear space at the posterior portion of the ventral margin of the foot. After removal of the style the incision was allowed to remain open, no suture apparently being necessary. Examination of the edges of the cut after two days showed that it had apparently healed.

FIG. 6.—The clam prepared for gastric registration, ventral aspect, showing the balloon tube entering the inhalent siphon and passing through the mantle cavity to the mouth. The light portion lying below the tube in the mantle cavity, and seen through the opening in the shell, is the foot.

In some of the animals studied a portion of the stomach wall was removed and immersed in a small amount of sea water. By sprinkling small grains of carmine in the water and observing with a dissecting microscope, ciliary action could be observed in the walls of the stomach. This is in accordance with the views of other writers on the subject (155) and it is also likely that the action of these cilia in the intact organ may set up definite fluid currents which may be an important aid to the processes of digestion and absorption in the clam. This idea is in agreement with the works of Irving (97), on the important activities of the starfish, concerning the distribution of food substance and the maintenance of tension in the pyloric cæca where the cilia serve the usual functions of muscular systems in other animals of correspondingly complex organization.

The results of this investigation give evidence of several rather interesting facts. In the first place, the technique developed seemed to be ade-

quate for the study of gastric movements in this clam. Simultaneous recording of the contractions of the foot was also possible with this method. As the foot contracted the movement was recorded on both the curve indicating stomach contractions and on the one indicating foot motion, but in the absence of foot movements the gastric contractions continued (Fig. 8 A and C). On an average, the stomach contractions occurred at the rate of one per minute, regardless of the presence or absence of the crystalline style, and the tonal changes were extremely slight.

FIG. 7.—The clam with neck contracted. The crystalline style has been removed and is shown below.

Studies made on the peristaltic activity of the stomach of the gaper clam by the balloon method, before and after surgical removal of the crystalline style, demonstrate unequivocally that the rotation of the style is not a substitute for gastric peristalsis (Fig. 8 A, B, C and D). This is contrary to the views of Nelson (*155*), Edmonson (*74*) and others who maintain that the style, among other things, functions in this way. The gastric contractions after removal of the style are practically identical with those obtained when it is intact, and in many animals they even become more vigorous in its absence. These contractions are continuous both in the presence and in the absence of the style and they show a definite relationship to the gastric activity observed in various gastropods which possess no crystalline style, namely: *Haliotis rufescens* (Abalone) ; *Ariolimax californicus* (Giant slug) ; and *Tethys californica* (Sea hare). The contractions are not the result of muscular movements of the foot, since they continue, uninterrupted, when the foot is quiescent. This is determined graphically by simultaneous records taken from the stomach and the foot (Fig. 8). Therefore, the musculature of the stomach of this animal produces the gastric contractions which places it in the same physiological category as the stomachs of other vertebrate and invertebrate animals studied.
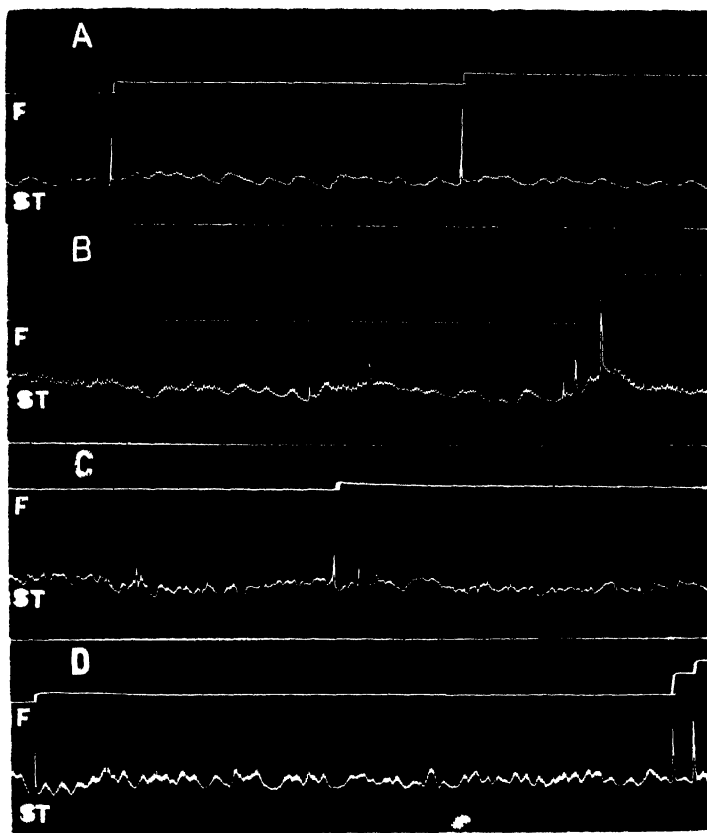
FIG. 8 —A, normal peristalsis, empty stomach of gaper clam, with a simultaneous record of the foot contractions, above, after a fast of 27 hours. B, same animal after surgical removal of the crystalline style and a fast of 46 hours C, normal peristalsis, empty stomach of gaper clam, with a simultaneous record of the food contractions, above, after a fast of 144 hours. D, same animal after surgical removal of the crystalline style and a fast of 161 hours. Note independence of gastric activity. St, stomach. F, foot.

AMPHINEURA

CHITON (*Cryptochiton stelleri*)

Little work has been done on this species and the chief studies, like those of Heath (*91*) on the excretory and circulatory systems, have been of an anatomical nature. *Cryptochiton stelleri* is the largest of the marine chitons and a most difficult form on which to work (*175, 176*). It is a vegetarian, characterized by its submerged chitonous plates, and the adult form in its antero-posterior plane measures from ten to twelve

inches.   The gastro-intestinal tube in this animal consists of a mouth,
buccal cavity, esophagus, a large, thin-walled stomach, and a long intes-
tine, the total length of which measures from five to six feet in the adult.
Since a gastric fistula was impracticable in this animal, it became necessary
to use a glass stomato-gastric tube, covered with rubber tubing, on the
end of which the recording balloon was attached (Fig. 9 B).   This
special tube was bent so as to fit into the mouth, the short esophagus, and
then into the cavity of the thin-walled stomach (Fig. 9 A).   It was
necessary to anesthetize the animal in a solution of two per cent. ether
in sea water, in a darkened chamber, in order to produce relaxation of the
muscles so the balloon with its special tube could be introduced into the
stomach for graphic registration of the gastric movements.   The animal,
in the anesthetized condition, was then placed on an oval stone in a large
vivarium provided with running sea water.   If this procedure is not
strictly followed the animal will "roll-up" into a hard mass and will re-
sist further experimentation possibly for fifteen to twenty hours.   Further-
more, if the air is let out of the stomach balloon and it is then reinflated,
or if the balloon's pressure is only slightly and very carefully increased,
it will cause the animal to "roll-up."

According to Arey and Crozier (7) this "rolling-up" reaction in chiton
has a purposeful aspect but the natural history of the animal yields no
evidence that this response is ever used.   These authors are of the opinion
that it is the outcome of the greatest maximal contraction on the part of
the chiton to produce suction, and that it is neither protective nor of the
nature of a reflex.   Such reactions may be produced by light (62) acting
on the sensitve ventral portion of the animal if the photic stimuli are
repeated.   Whatever may be the proper explanation for this reaction, it
is most essential that the tactile irritation be reduced to the lowest possi-
ble level and this can be produced best by carrying out the anesthetization
in a darkened chamber.

THE MOVEMENTS OF THE EMPTY STOMACH

The gastric contractions as observed in this animal were continuous
with only a very slight indication of an altered periodicity (Fig. 10 A).
They appeared to be analogous with the twenty-second rhythm in man.
Furthermore, the stomach, when partially filled with food, exhibited the
same type of activity.   The gastric hunger activity may be inhibited by
mechanical or chemical stimulation of the sensory surfaces of the animal,
such as touching the dorsal or ventral edges of the mantle with a glass

seeker or by the introduction of a one per cent. solution of sodium carbonate into the water near the edge of the mantle (Fig. 10 B, C', D and E). Movements of the animal will also cause inhibition.
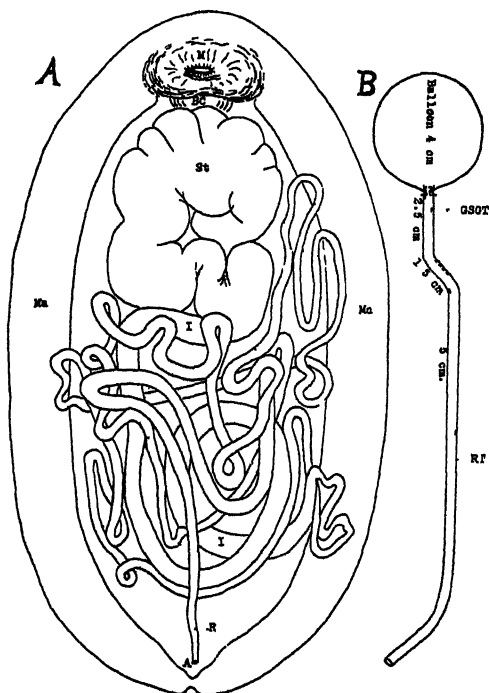
FIG. 9.—A, ventral aspect, gastro-intestinal tract of *Cryptochiton stelleri* (5½ feet in length in adult). M, mouth. BC, buccal cavity. St, large, thin-walled stomach. I, intestine. R, rectum. A, anus. Ma, mantle. B, special rubber balloon. GSGT, glass stomato-gastric tube inside rubber, to fit into mouth and short esophagus. RT, rubber tube connecting with water manometer.

GASTROPODA

ABALONE (*Haliotis rufescens*)

In addition to the morphological studies on the European Haliotidæ, Lacaze-Duthiers (*116*) worked on two species of large gastropods, *Haliotis lamellosa*, found on the coast of the Mediterranean, and *Haliotis tuberculata*, found on the coast of Brittany, a province of Western France bordering on the English channel and the Atlantic Ocean. This investigator made a study of the nervous systems of those two forms and directed attention to the stomato-gastric nervous system which alone is destined to supply the vital activity to the gastro-intestinal canal. The ganglionic centers of this stomato-gastric nervous system are situated in the Haliotidæ as in other gastropods under the first portion of the digestive tube, the latter occupying a dorsal position.
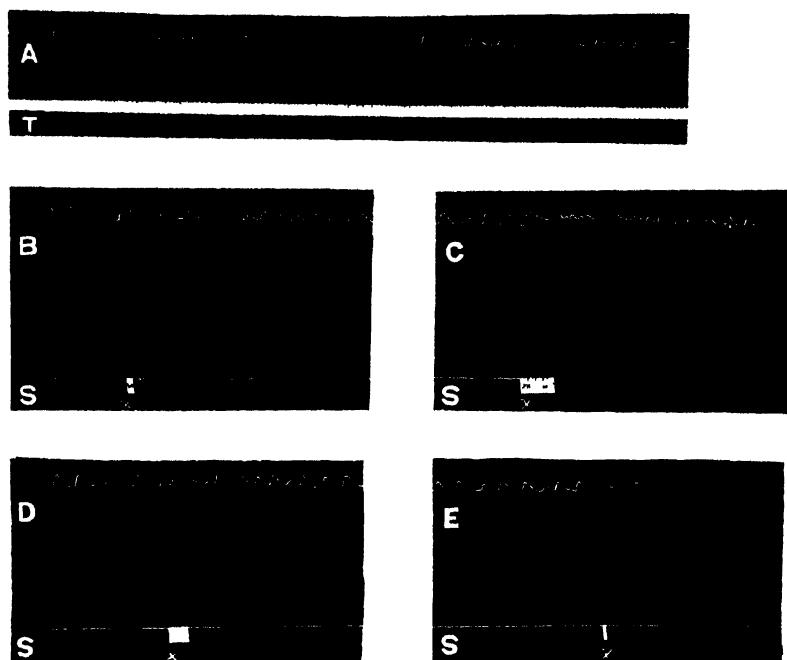
FIG. 10.—Gastric contractions of the stomach of *Cryptochiton stelleri*. A, normal peristalsis, empty stomach of Cryptochiton after a fast of 20 days. B, temporary inhibition from slight stimulation of dorsal edge of mantle   C, same with longer continued stimulation   D, same from stimulation of ventral edge of mantle. E, complete inhibition from introduction of 5 cc., 1 per cent. sodium carbonate solution on edge of mantle, anterior portion. T, time intervals in seconds. S, signal.

The work on *Haliotis rufescens* (*175, 176*), as in the case of other marine forms studied by the writer, and herein described, was conducted at the marine station of Stanford University at Pacific Grove, California, on Monterey Bay.

THE MOVEMENTS OF THE EMPTY STOMACH

This particular species is the popular edible, univalved shell-fish of the Pacific Coast (Fig. 11). Californians will travel afar for a portion of Abalone steak or chowder. The adult of this species may attain a length of eight to nine inches and is a most suitable animal for studies on gastric motility. The technical procedure consisted of raising the anterior portion of the shell when the foot was firmly attached, thus putting the tissues on the stretch and exposing the esophagus beneath. An esophageal fistula was then made about five centimeters posterior to the mouth by

making a small transverse incision laterally with scissors through the exposed wall of the esophagus. The balloon was introduced through this opening and pushed into the stomach, and the rubber tube for the mano-meter then carried through one of the fissures in the shell (Figs. 11 and 12). The contractions always started in twelve to fifteen minutes follow-ing this procedure and were continuous at the rate of about four per minute. These contractions occupied a period of about ten seconds for their completion and were followed by a rest period averaging about five seconds. However, a certain type of altered periodicity was noted, as indicated by periods of marked activity separated by periods of strong hunger contractions; the individual contractions in the latter case had comparatively long intervals of rest of about eighty seconds between them, but the contractions, although of somewhat greater amplitude, were of normal duration. The periods of altered activity usually lasted from twenty-five to thirty minutes (Fig. 13 E). In starvation, the gastric con-tractions progressively increased in strength until after about two weeks, when they approached the form of incomplete tetanus (Fig. 13 C). The gastric activity, therefore, increases in vigor in proportion to the duration of the fast, as is shown by a comparison of the normal digestive peristalsis (Fig. 13 A) with that of the fasted stomach (Fig. 13 B and C).

THE INHIBITION OF THE GASTRIC MOVEMENTS

The introduction of sea-water, fresh tap water, one per cent. sodium car-bonate, or 0.5 per cent. hydrochloric acid, directly into the stomach, pro-duced inhibition in varying degrees, the intensity being indicated in the order of the respective substances as given (Fig. 14 A, B, C and D). It was the least in the case of sea water and the greatest with the acid. In fact, both mechanical and chemical stimuli, when applied to the sensory surfaces of this animal, as the mantle, epipodia, sense palps, etc., invari-ably produced temporary inhibition of the gastric hunger movements; but its duration did not usually exceed greatly the duration of the actual stimulation unless it was severe. Movements of the animal also tended to inhibit the contractions of the empty stomach (Fig. 13 D).

In respect to chemical stimuli, it is interesting to note the protective mechanism of the animal. When small quantities of a one per cent. solu-tion of sodium carbonate or a 0.5 per cent. solution of hydrochloric acid are introduced into the water near the palps and epipodia, or at the anterior or posterior regions of the body, the animal will almost immediately raise its shell and then quickly and forcibly draw it downward, followed almost

Fig 11.—Shows *Haliotis rufescens* (Abalone) with two rubber tubes passing through one of the fissures in the shell, to enter the esophageal fistula (not shown). The shorter tube, having a gastric balloon attached to the end, connects with a recording water manometer. The longer tube is for the introduction of fluids into the stomach, to determine the effects of inhibition.

invariably by three vigorous, forty-five degree, rotary movements, the order of rotation usually being left, right, left. These reactions set the water in motion around the animal, and expel it from beneath the edges of the shell, thus washing off the irritating alkali or acid. Mechanical stimulation, such as may be produced by working around the animal, may also cause rotary movements if the stimuli are of sufficient strength.

Furthermore, the introduction of 5 cc. of a 0.5 per cent. solution of hydrochloric acid directly into the stomach via a second rubber tube, not only produced temporary inhibition but it usually led in five to ten minutes to an actual increase in the strength of the gastric contractions,
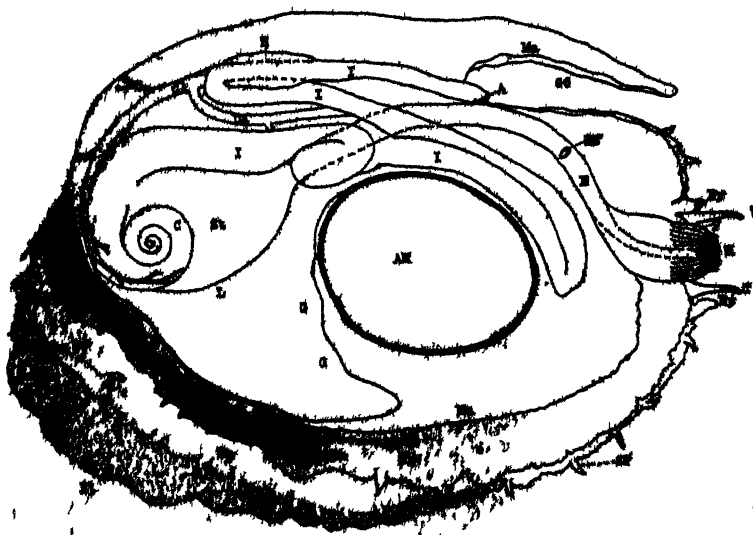
Fig. 12 – Shell of *Haliotis rufescens* (Abalone) removed to show anatomical arrangement of organs and other structures. M, mouth; P, proboscis, E, esophagus; EF, esophageal fistula; St, stomach; C, cæcum; I, intestine; A, anus; L, liver-pancreas; G, gonad; H, heart; DA, dorsal aorta; GA, gastric artery; AM, adductor muscle; Ma, mantle; Ep, epipodium; Sp, sense palp; Ft, foot, Ey, eye, T, tentacle, GC, gill chamber

the strong contractions ranging in height from three-quarters to one and one-quarter inches. During these strong contractions there was expelled from the end of the anal canal a liquid substance which probably contained some mucous. This substance produced a white precipitate in the sea water at the moment of expulsion and revealed on closer examination that it was squirted out with considerable force as a small stream which shot

FIG. 13.—Gastric contractions of the stomach of *Haliotis rufescens*. A, normal digestive peristalsis   B   normal peristalsis of empty stomach after a fast of 10 days. Note the increased vigor of the contractions as illustrated by the amplitude.   C, hunger peristalsis after a fast of 16 days, indicating an incomplete tetanus of the gastric mechanism.   D, inhibition from body movements.   E, hunger peristalsis after a fast of 10 days, showing the termination of a period of marked activity followed by strong hunger contractions, separated by comparatively long intervals of rest, and indicative of an altered periodicity.

out an inch or more from the anal orifice into the sea water. More careful analysis of the above showed further that the gastric contractions appeared on an average about one second previous to the actual expulsion of any substance from the anal opening, as determined by the formation of the white precipitate, in the sea water, which soon disappeared. The expulsion of the substance invariably commenced on the rise of the curve, at a point one-half to two-thirds of the way up. This period of expulsion may be of longer or shorter duration, lasting from seven to twenty-one seconds as determined by the time from appearance to disappearance of the precipitate in the sea water. In some cases, the first expulsion was followed by a second expulsion period, ranging in time from 0.5 to 5 seconds and separated by an interval of from seven to eighteen seconds; the second expulsion period was usually of shorter duration than the first. These strong contractions will sometimes continue five to six hours following the injection of the hydrochloric acid and will exhibit a more or less definite regularity. The probable explanation for this reaction is, no doubt, that it is caused by the acid setting up a local reflex stimulation of the gastro-intestinal canal.

In general, the automatic movements of the empty stomach of *Haliotis rufescens* falls in line with the gastric activity of other molluscs herein discussed.

Sea Hare (*Tethys californica*)

The sea hare or sea rabbit is a most interesting animal (*239*). It derives its popular name from the prominent character of the front pair of tentacles, which somewhat resemble the ears of a hare. The species employed in this study is devoid of any shell. It is another large marine mollusc and may attain a weight of fifteen pounds or more. It is also a vegetarian, feeding chiefly on *Zostera* (kelp) and, judging from its wholesale ingestion of this substance and the efficiency of its gastric mill, *Tethys californica* converts vegetable material to animal matter at a rather rapid rate.

During the period of gastric observation this animal spawned, the large egg mass which was attached to the side of the aquarium resembling a great tangle of yellow yarn. The number of eggs oviposited by this marine species is of interest and MacGinitie (*128*), in one case, calculated that the egg string was 61.2 meters in length, contained 83,350,344 eggs, and weighed 1937 grams.
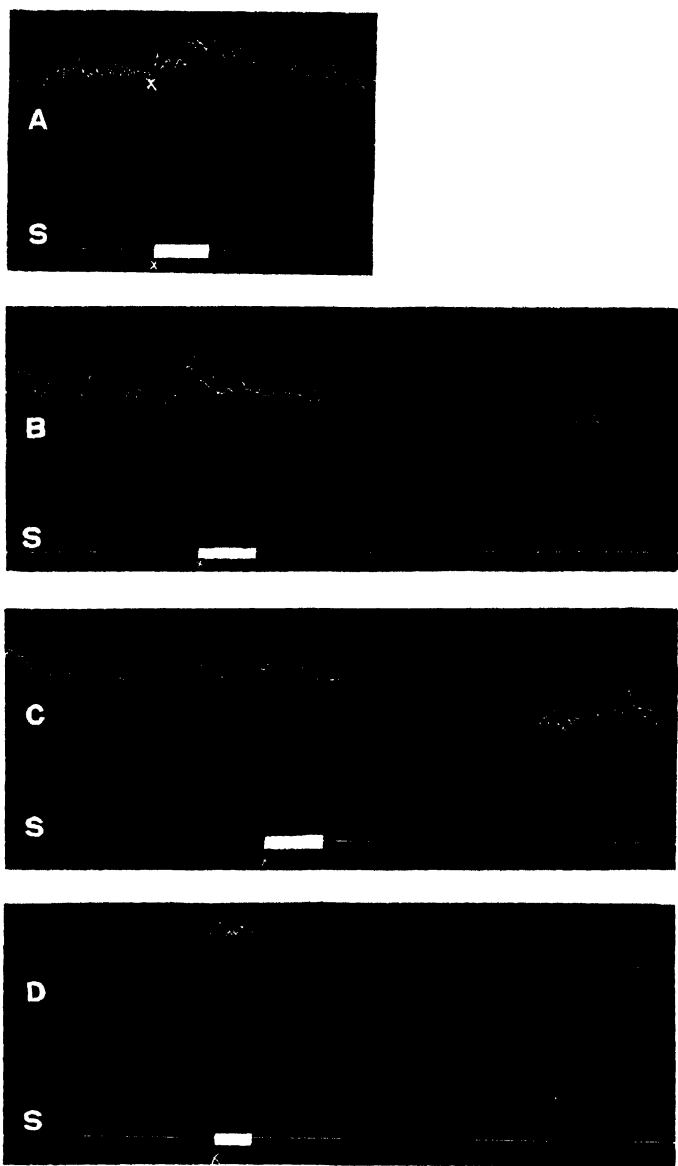
FIG. 14.—Inhibition of the gastric contractions in *Haliotis rufescens* after a fast of 10 days. A, introduction of 5 cc sea water directly into stomach at x. with practically no effect. B, inhibition from introduction of 5 cc. fresh tap water directly into stomach at x. C, alkali inhibition from introduction of 5 cc. 1 per cent. sodium carbonate solution directly into stomach at x. D, acid inhibition from introduction of 3 cc. 0.5 per cent. hydrochloric acid solution directly into stomach at x. S, signal.

The automatic rhythmical movements of the esophagus of the European sea hares, *Aplysia depilans* and *Aplysia limacina* were studied by Bottazzi (*20, 21*). He found that the esophagus of the former, when excised and placed in a moist chamber, executed automatic contractions at the rate of fifteen to sixteen per minute, and instituted a regular or irregular

FIG 15.—The sea hare with rubber tubes and balloon passing through mouth and esophagus to stomach, ready for gastric registration. Dorsal aspect of animal

rhythm which persisted through many hours. These rhythmic movements he regarded as of a purely myogenic nature. In *limacina*, he found the esophagus not only to be normally more flaccid and atonic, but that the spontaneous movements which it exhibited were transient and sometimes difficult to register. However, the entire musculature of the body of this species is atonic as compared with that of *Aplysia depilans*. Brücke (*25*) also worked on the spontaneous movements of the isolated esophagus of *Aplysia depilans* and found that these movements were dependent upon the degree of the repletion of that organ.

THE MOVEMENTS OF THE EMPTY STOMACH AND THEIR INHIBITION

The introduction of the balloon into the stomach of the California species of sea hare was accomplished by anesthetizing the animal in a solution of two per cent. ether in sea water and passing a balloon and the attached tube down the esophagus while the animal's muscles were relaxed (Fig. 15). The movements of the empty stomach of this animal

were continuous and exhibited an average rate of five to six contractions
per minute. There were also rather marked variations in tonus, which
the writer is inclined to believe were caused chiefly by the stomach mus-
culature, although it is possible that there may have been slight effects
produced at certain intervals through the body musculature even when
the animal was apparently quiescent. Otherwise, the animal presented
the same general characteristics as those already described in the other
forms of animals under this class, and particularly that of the Abalone,
except that the contractions were somewhat stronger, the height being
dependent on the duration of the fast (Fig. 16 A, B and C). The same in-
hibitory action on the gastric contractions from the introduction of weak
acid or alkali was also exhibited as in other animals studied (Fig. 17).
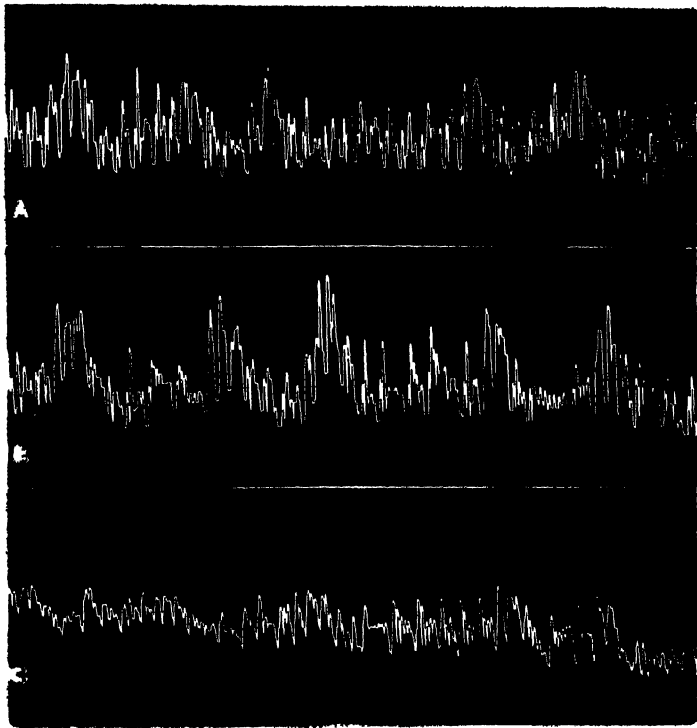
Fig. 16.—A, normal peristalsis, empty stomach of sea hare or sea rabbit (continuous
activity), after a fast of 346 hours. B, same animal after a fast of 358 hours. Note
periods of incomplete tetanus and increased amplitude of contractions. C, same animal
after a fast of 624 hours, showing stomach to be virtually in a stage of incomplete tetanus.
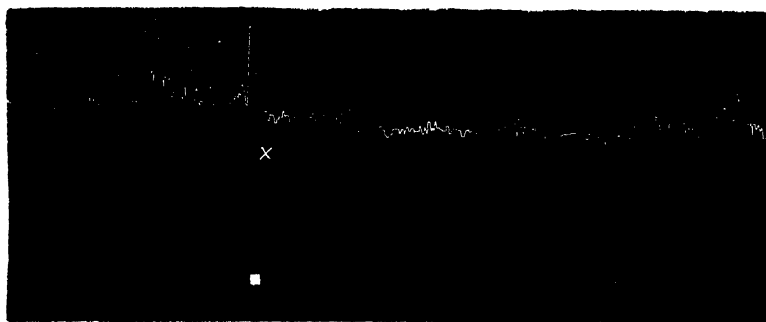
FIG. 17.—Alkali inhibition from introduction of 10 cc. 1 per cent. sodium carbonate solution directly into stomach of the sea hare at x.

GIANT SLUG (*Ariolimax californicus*)

Ariolimax californicus, the giant slug, was the only terrestrial type of mollusc studied. These animals inhabit the forest, where the sun's rays hardly penetrate to the surface of the earth, and where the ground is covered with moulding trunks of trees and thick layers of decaying leaves, all of which favor a constant moisture which are so essential for the welfare of these animals. In seasons when they become abundant they may cause much damage in gardens and orchards. They seek their food at night and are nocturnal or semi-nocturnal in their habits. They may be found hiding under fallen trees, stones, etc., or during the day may wholly or partially bury themselves in the earth where they remain inactive. In seasons of drought they penetrate deeply into the earth. The adult animal may attain a length of fifteen centimeters. Binney (*15*), in his morphological studies on this species of *Ariolimax,* found that the orifice of the mouth opened into the cavity of the buccal body, the latter of which is an irregular, oval shaped, muscular organ, resembling in appearance a gizzard, and containing within it the masticating apparatus. According to this investigator the esophagus leads from the upper posterior part of the buccal body back to the stomach; it is short and dilates into the latter, which extends two-thirds the length of the body. Furthermore, Pilsbury and Vanatta (*188*) found that the alimentary canal of this animal is distinctly differentiated into fore, mid, and hind, gut. The short esophagus leads into a capacious crop which is separated by a decided constriction from the stomach. In the present investigation, for the sake of convenience the stomach has been divided into three main parts, the cardiac, intermediate and pyloric portions (Fig. 18). The esophagus is separated from the cardiac portion by a constricted ring of tissue and is

short and straight. Another constricted ring of tissue also separates the intermediate portion from the bag-like pylorus. Actual measurements of the alimentary tube show it to have a length of thirty centimeters or more.

Part of the animals employed in this study were collected at Roble's Bridge on the Stanford University campus, Palo Alto, California, and the remainder at Strawberry Canyon on the University of California campus, Berkeley, California. The animals were shipped to Detroit by express in a special shipping box having a compartment which was kept filled with ice. Following their arrival, they were kept in the basement of one of the college buildings where it was cool, and fed on cabbage or lettuce leaves with bread crumbs added twice weekly. Water was sprinkled over the leaves daily to provide the necessary moisture. Under such conditions the animals would live for an indefinite period.

THE INFLUENCE OF LIGHT AND DARKNESS ON ANESTHETIZATION OF THE ANIMAL

The technique employed for the study of the movements of the empty stomach in this great land snail was similar to that used on the *Cryptochiton,* with the exception that a smaller balloon and tube were necessary because of the smaller size of the animal. In this case, however, no stomato-gastric glass tube was required and a rubber tube four millimeters in diameter could be passed through the opening in the esophagus. This was also a difficult form on which to work.

The most effective technique for the introduction of the balloon was to anesthetize the animal with chloroform in a darkened chamber. For some reason this type of anesthetic seemed to be more effective than ether in producing greater muscular relaxation. The effect of darkness on the animal during the period of anesthetization was also of the utmost importance as already shown in the anesthetization of *Cryptochiton* and also by the work of Crozier (62) and Arey and Crozier (7) in reducing tactile irritation or stimulation by light to the lowest possible minimum which brings about greater relaxation of the body musculature. The importance of the influence of darkness on the muscular relaxation of these animals during anesthetization is well illustrated by the following experiment. Two healthy individuals were selected, one of which was anesthetized in a bright light, while the other was placed in a darkened chamber. The one in the bright light contracted its body musculature to such an extent as to rupture its body wall through which the viscera protruded, while the one anesthetized in the darkened chamber was fairly well relaxed. When the animal became relaxed it was removed from the anesthetic chamber
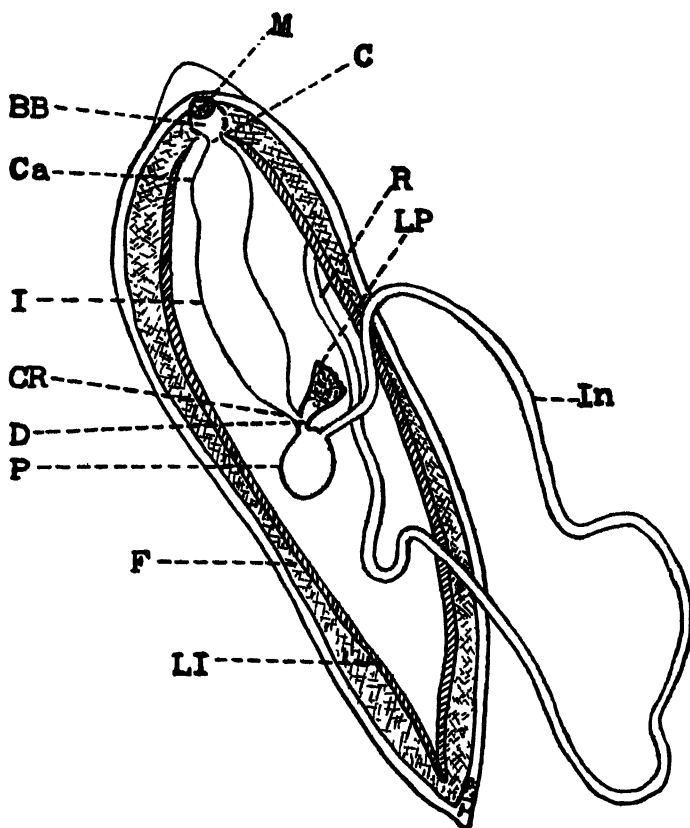
Fig. 18 — Ventral aspect, gastro-intestinal tract of *Ariolimax californicus*. M, mouth. BB, buccal body. Ca, cardiac stomach. I, intermediate stomach. P, pyloric stomach D, duct of liver-pancreas. F, foot. LI, line of incision through foot. In, intestine. R, rectum LP, liver-pancreas. C, constricted ring of tissue separating buccal cavity from the cardiac portion of the stomach. CR, constricted ring of tissue separating the intermediate and pyloric portions of the stomach.

and cotton was wrapped entirely around the animal with the exception of a cone-like opening left for the head. The cotton cone was used for holding the animal during the introduction of the balloon, requiring usually ten to fifteen minutes. This is a very slow process since the balloon must be worked into the mouth by manipulating with the fingers the end of the tube on which the small balloon is attached; eventually the animal tends to engulf it. With this part of the procedure completed, the cone was easily removed, since the copious secretion from the actively secreting mucous membrane forms a smooth inner lining to the cone. The animal was then placed in a box somewhat darkened by its sides, with suitable moisture,

and was ready for gastric registration, either a small water manometer or a tambour being used. The earlier records from the stomach were complicated by the foot or pedal movements. Better to control the experiment, the opaque bottom of the box containing the animal was replaced by a plate of transparent glass, all of which was supported on a stand with a mirror adjusted directly below, in order that any pedal movements might be detected in the mirror during the registration of the gastric contractions. While this improvement in technique was of great advantage in detecting pedal movements, and although at times gastric contractions were indicated which appeared to exhibit a more or less definite rhythm, they were not of sufficient duration or constancy, in the opinion of the writer, absolutely to demonstrate gastric contractions. In addition to the pedal musculature, the body musculature must also be taken into consideration, both of which tend to complicate the recording of the gastric activity in this animal.

X-RAY STUDIES ON THE GASTRIC MOTILITY

As a further means of studying the gastric activity in *Ariolimax,* one of the animals was fasted for two days and then placed in a beaker containing a fresh cabbage leaf sprinkled with fine bread crumbs and bismuth subnitrate plus a little water to maintain the necessary moisture. After the animal had fed on the leaf preparation it was suspended in a rolled sheet of paper and attached to the top of a fluoroscopic frame. The outline of the pyloric portion of the stomach was visible and peristaltic waves were observed passing over it at the rate of about one every twenty seconds. The duration of the actual contraction averaged six seconds, followed by an average rest interval of fifteen seconds, giving approximately a twenty second rhythm comparable to that observed in the *Cryptochiton.* No peristaltic activity was observed in the cardiac and intermediate portions of the stomach, since the outline of these was indistinct.

The animal was permitted to feed on the preparation during the night. On the following morning the mouth was somewhat protruded and the radula organ could be observed at times, but this was withdrawn later in the day. During the day and the next night the *Ariolimax* ingested a little more of the leaf preparation with the result that on the following morning the stomach was completely protruded through the mouth and exhibiting definite peristaltic movements (Fig. 19). The peristaltic waves appeared to start at the cardiac end of the stomach, spreading over the intermediate portion and then passing into the pylorus at a regular and definite rhythm.

The duration of the peristaltic waves observed over a period of thirty minutes and at a temperature of 27° C. was found to range from five to nine seconds, with an average of six seconds followed by an average interval of rest of fifteen seconds. Therefore, the rate of the contractions as revealed by this animal are in general agreement with the rate and duration of those observed by the X-ray. This was the only animal fed bismuth subnitrate and the only opportunity afforded for studying the protruded stomach; however, typical gastric waves exhibiting the same rate and duration were maintained for several hours. In other experiments of this

Fig. 19.—Giant slug with stomach protruded through mouth after ingesting bismuth, showing the same type of gastric contractions as observed by the balloon and X-ray methods.

nature instead of the bismuth subnitrate, there was substituted barium sulphate which proved to be more agreeable to the animal. However, X-ray studies of the stomach following the ingestion of barium sulphate revealed identical results.

Brücke (*25*) has reported that the rhythmical spontaneous movements of the isolated esophagus of *Aplysia* are dependent upon its degree of repletion. Furthermore, ten Cate (*232*), working on the isolated stomach of snails, *Helix pomatia* and *Helix aspersa*, in aërated Ringer's solution, found that the rhythmical spontaneous movements of the stomach were largely dependent on the degree of repletion and the state of tonic contraction of the organ.

In several experiments, in which the intact stomach was exposed by a longitudinal incision through the mid-portion of the foot and the entire animal then placed in oxygenated Ringer's solution, no contractions were exhibited by either the thin walled cardiac or intermediate portions.

But when the balloon was pushed down into the thick-walled, sac-like pylorus, active movements were exhibited, which were readily recordable on a kymograph making a revolution in sixty minutes. These movements were also observable by the method of direct inspection in the absence of any balloon in the stomach. It is, therefore, probable that the balloon method is not sufficiently delicate to register the spontaneous activity in the thin walled portions of the stomach since they are doubtless stretched to the point of functional injury in the absence of intra-abdominal pressure which was destroyed by the incision through the foot.

STUDIES ON FASTED AND NON-FASTED ISOLATED STOMACHS

In a further series of studies made on the isolated stomach, which was carefully prepared without injury, and divided into two portions, namely, cardiac plus intermediate, and pylorus, respectively, it was found that when these preparations were attached to separate light heart levers of the Harvard type and placed in oxygenated Ringer's solution, both preparations exhibited rhythmical spontaneous movements; but those of the pylorus were much more vigorous than those exhibited by the cardiac-intermediate portion. The technique consisted of tying a silk thread around the intestine and the constricted portion lying between the intermediate and pyloric portions, and close to the pylorus, the opposite end of the thread then passing to the lever, while the lower bag-like end of the pylorus was attached to a fixed support, the silk thread being attached to the serosa. The two ends of the cardiac-intermediate portion were similarly attached to another lever. Such preparations may continue to exhibit spontaneous activity for many hours. The contractions in both of the preparations were continuous and of approximately the same rate, but the amplitude of the pyloric contractions were considerably greater than those of the cardiac-intermediate portion. Observations were also made by this method, using chiefly the pyloric portion of the stomach on preparations obtained from animals in a good state of repletion, and from those in the fasting condition. The stomachs obtained from animals in a good state of repletion contained a brown, jelly-like material which was carefully removed. In all cases the fasting stomach exhibited the more vigorous activity as shown by the greater amplitude of the contractions (Fig. 20 A and B).

THE EFFECT OF INSULIN AND GLUCOSE ON THE GASTRIC ACTIVITY

This greater activity on the part of the fasted stomach according to Bulatao and Carlson (27) is thought to be referable to a reduction of available glycogen which causes the stomach to respond with more strength

and greater amplitude than is found in the well nourished organ. In the conditions found to increase gastric hunger contractions in higher animals there is either a decrease in tissue glycogen (starvation, muscular exercise, phlorizin), or inability of the tissues to burn sugar (pancreatic diabetes). Since increased hunger is one of the symptoms accompanying insulin hypoglycemia in man, it would seem to point to the availability of carbohydrates for utilization by the stomach motor tissues as being an important factor in the genesis or intensity of the gastric hunger contractions. These investigators, working on dogs, have found that the subcutaneous administration of insulin is accompanied by increased gastric tonus and hunger contractions, while an intravenous injection of glucose inhibits the gastric hunger tetany of hypoglycemia. Very little work has been done
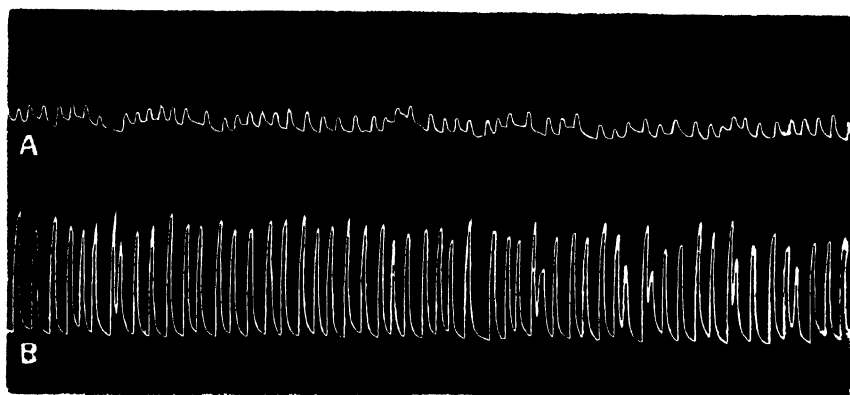
FIG. 20.—A, extirpated stomach in oxygenated Ringer's solution, obtained from a well nourished animal during digestion. B, extirpated stomach in oxygenated Ringer's solution, fasted 402 hours. Note the more vigorous activity of the fasted stomach.

with insulin on invertebrate animals. Karásek (*106*) has studied its effect on the contractility of the tentacles of sea anemones. He found that when one-tenth milligram of insulin was added to twenty cubic centimeters of sea water the contractility of the tentacles was increased for a short time and then decreased afterward for an hour. The addition of glucose had the opposite effect, which was enhanced by the simultaneous use of both insulin and glucose. Because of the limited amount of work in this field it seemed of sufficient importance to determine the influence of insulin and glucose on the isolated stomach of the giant slug. The same technique was employed as described above, and the two preparations to be tested were placed in oxygenated Ringer's solution. The insulin or glucose, as the case might be, was injected directly into the cavity of the stomach

with a small hypodermic needle, the needle being introduced through that portion of the gut wall directly below the attachment of the silk thread to the lever. The careful introduction of the needle alone did not cause any reaction of the stomach. "Iletin" (Insulin Lilly) was used for the experimental work. The introduction of .067 cc. of U-10 iletin directly into the stomach from the well nourished animal led to a marked augmentation of the gastric tonus, lasting for many minutes, whereas the same amount of a 25 per cent. solution of glucose produced an inhibitory effect in the
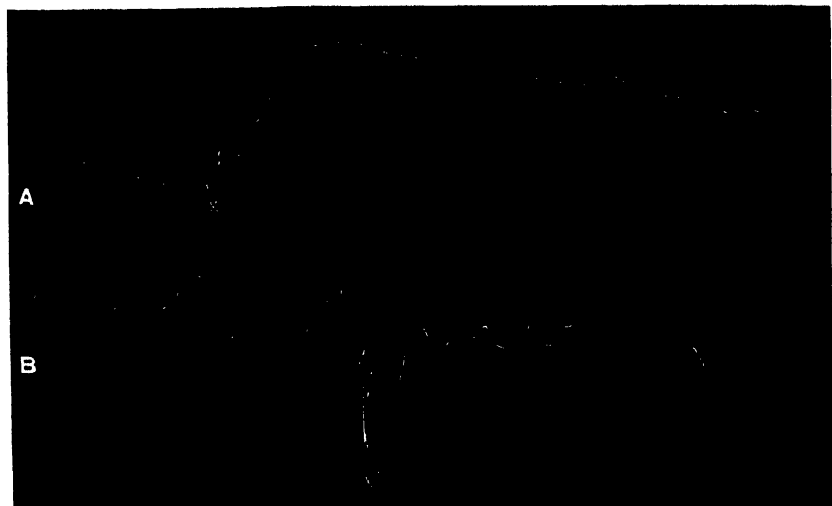
FIG. 21.—A, unfasted stomach in oxygenated Ringer's solution with introduction of about .067 cc. of insulin U-10 directly into the extirpated stomach, showing a marked augmentation in the gastric tonus. B, fasted stomach with introduction of about the same amount of a 25 per cent. glucose solution directly into the extirpated stomach. Note the inhibitory action of glucose on the fasted stomach.

fasting stomach which was exhibiting marked gastric activity (Fig. 21 A and B). The same reactions were obtained when the cardiac-intermediate portion of the stomach was used and although the gastric activity was of a lesser degree, yet the same responses from the well nourished and fasting stomachs resulted from the use of iletin and glucose. With .067 cc. of U-20 iletin the reaction is more marked in both cases, the period of increased tonus lasting from 20 to 40 minutes depending upon whether the U-10 or U-20 strength of iletin is used. The results of insulin and glucose on the gastric activity of this invertebrate animal are in agreement with those obtained on dogs, and again would seem to indicate the

importance of carbohydrates as a controlling factor of the gastric hunger contractions.

THE INFLUENCE OF TEMPERATURE ON THE GASTRIC ACTIVITY

Considerable work has been done on the influence of temperature on the activity of various tissues and organs. Cameron and Brownlee (*29*) and Cameron (*28*) have reported that frogs freeze at a temperature of −0.44° ± 0.02° C. in a manner very similar to that of solutions isotonic with their body fluids. Specimens of *Rana pipiens* obtained from the vicinity of Chicago will survive a temperature of −1° C. but they will not survive a temperature of −1.8° C. The exsected hearts of these animals will survive a temperature of −2.5° C. for one hour, but are killed by a temperature of −3.0° C. for one hour. Britton (*23*), working on temperature effects on fishes, at the Canadian Government Atlantic Biological Station at St. Andrew's, N. B., found that they survived exposure to water at temperatures −1° to −2° C. from one to several hours. In this period all the vital activities gradually diminished and eventually disappeared, the heart beat being the last to cease in diastole. Fishes exposed to a water temperature of 25° C. were but little affected, whereas 30° C. produced much distress, and death soon followed unless a reduction in the water temperature was made. In *Necturus,* maximal gastric activity occurs at about 18° C., while much above or below this temperature there is diminution in the rate and amplitude (*174, 178*). For reduction of temperature they cease completely at 7° C. In the bullfrog, maximal gastric activity occurs between 15° C. and 32° C. The contractions of the empty stomach are completely inhibited at 35° C. for maximal temperature, and 13° C. for minimal temperature. Decreasing the temperature in the former or increasing it in the latter, 0.5° C., or at the most 1° C., will cause the return of the gastric contractions (*168*).

Studies on temperature effects were carried out on the isolated stomach of *Ariolimax californicus* in oxygenated Ringer's solution. At 18° C. the stomach preparations were most responsive and exhibited the greatest maximal activity. Cessation of activity occurred on raising the temperature to 37° to 38° C., the contractions decreasing in amplitude and finally stopping at 38° C. for the fasted tissue. Reduction in temperature caused the fasted tissue to cease its activity at −3° C. The stomach preparations obtained from animals in a good state of repletion usually ceased their activity from one to two minutes sooner than in the case of the fasted preparations. These temperature changes were gradual, and

extended over a period of two and one-half hours. In applying van't Hoff's rule to this work, the data shows that the relation between contractions and temperature is maintained either when the stomach preparations pass from a lower to a higher temperature or vice versa; the rule being that for each increase of 10° Centigrade, the velocity of a reaction is doubled or trebled. This rule, while it usually refers to chemical reactions, may also be applied to the physiological reaction of animal tissues as exhibited between certain not very wide ranges of temperature.

Tables I and II show the results obtained from experiments on fasted stomach preparations in oxygenated Ringer's solution, with the respective number of contractions executed in the unit of time. Temperature coëfficients were obtained as quotients from the formula used by Riddle (196):

<div align="center">Rate at Tn</div>

<div align="center">Rate at T x</div>

Tn is the higher temperature, T the lower temperature, and X the difference between these two.

<div align="center">TABLE I</div>

<div align="center">Raising the Temperature</div>

Number of contractions per 7 min. intervals— room temperature	Number of contractions per 7 minute intervals after increase of temperature	Temperature coefficient
26° C. = rate of 8	32° C. = rate of 13	2.70 +
26° C. = rate of 8	33° C. = rate of 21	3.75 +
23° C. = rate of 12	30° C. = rate of 16	1.90 −

<div align="center">TABLE II</div>

<div align="center">Lowering the Temperature</div>

Number of contractions per 7 min. intervals— room temperature	Number of contractions per 7 min. intervals after decrease of temperature	Temperature coefficient
26° C. = rate of 42	20° C. = rate of 18	3.88 +
26° C. = rate of 42	14° C. = rate of 12	2.91 +
21.5° C. = rate of 21	14° C. = rate of 10	2.66 +
21.5° C. = rate of 21	10° C. = rate of 9	2.03 −
22° C. = rate of 16	11° C. = rate of 6	2.42 +

The results of this investigation show conclusively that the contractions are not only continuous in both the fasted and unfasted preparations, but that the fasted stomach exhibits a greater degree of regularity than that obtained from the stomach preparation in a state of repletion. Furthermore, the contractions from the fasted stomach were of greater strength and amplitude, and this applies to all three portions of the stomach. Slight variations in the tonus were also observed. In general, the stomach's activity observed in this species is in agreement with similar work on other molluscs. Furthermore, experiments have shown that live animals in a good state of repletion, with plenty of moisture, will withstand a fast of from 33 to 35 days.

TYPES OF VERTEBRATA STUDIED

CHORDATA

CYCLOSTOMES

HAGFISH (*Polistotrema stouti*)

The hagfish is, with the exception of amphioxus, the lowest of the vertebrates. It is eel-like in form and feeds upon fishes, boring into their bodies and devouring their viscera and flesh, and is a most destructive agent of the commercial fisherman who undertakes to use set gear in localities, such as Monterey Bay, California, where they occur in great abundance. This animal is about eighteen inches in length, and is semi-parasitic in habit. It is easy to catch in traps and may be kept in an aquarium for a considerable period of time. A simple device, described by Greene (*88*), is to take a five-gallon oil can and puncture it with a number of small holes just adequate to admit the passage of a hagfish. The sharp, jagged edges of the tin around these holes on the inside will act to retard the exit of the fish. A liberal quantity of dead fish is introduced for bait through a trap door which is made secure, and then the trap is taken about one hundred yards off shore from the Marine station and lowered to the bottom of the bay. Under the most favorable conditions the can may be completely filled with hagfish. However, some may escape while the trap is being drawn to the surface, but even then it is not uncommon to obtain from fifty to seventy specimens from a single haul.

The eyes are rudimentary, but in compensation for the blindness the animal appears to be endowed with a keen sensitiveness both to physical contact and chemical stimuli. In the case of chemical stimuli the entire

reaction of the animal is a splendid illustration of the chemical guidance of a blind carnivorous and parasitic fish.

The California hagfish is unique among animals in possessing more than one heart. It is generally known that the eels of the rivers of the Atlantic seaboard and of the Mississippi Valley have, in addition to the usual systemic heart, a contractile vascular organ in the tail, on the caudal vein. The hagfish, however, has three hearts. In addition to the systemic and caudal hearts, Jackson (*101*) has found a third heart located in the portal venous system with incoming and outgoing vessels all adequately provided with valves to insure a one-way course of the blood. Furthermore, Greene (*87, 88*) has reported that there are no cardiac regulative nerves in the vagus for either the systemic or portal hearts. However, the caudal heart varies from the above in that the walls of the cavity itself are non-contractile and that the caudal pump derives its power from a pair of skeletal muscles differentiated out of the great lateral muscles of the region, and is, like all skeletal muscles, innervated from the spinal cord.

According to Herrick (*92*) the brain of the hagfish is organized around two dominant sensory systems, the olfactory nerve and the trigeminal nerve, in which are located the senses of smell and touch; the other special senses are in various stages of degeneration. There are vestigial eyes and no jaws or limbs, and the typical response to almost any kind of an adequate stimulus is a wriggle involving practically the entire body. The two senses of smell and touch are very highly developed and the simple motor mechanism is activated mainly from these two sources of excitation. Although the complexity of the brain of the hagfish is of a different pattern from that of a higher animal, it cannot be considered as consisting of a few separate reflex arcs; it possesses a structure peculiar to itself. In fact, it is only from the developmental and functional side that the question can be properly analyzed. The animal lives a very simple and uneventful life and each stimulus that comes in must be transmitted to muscles all over the body, as an order to move. Hence, the apparent random branching of the nerves, and their distribution, is described as a "hay-wire" pattern, for the fibers from this whole pattern converge into the muscles causing mass movements over the entire body.

THE INFLUENCE OF THE VAGUS NERVE ON THE STOMACH-INTESTINE

Johannes Müller (*153*) has described the vagus nerve of the hagfish as sending branches to the gill sacs, to the heart, and to the stomach-intestine. This author (*152*), nearly a hundred years ago, in 1837, wrote

that in the *Myxinoides* the Rami intestinales developed out of the union of both vagi and ran as far as the rectum, while the sympathetic was entirely absent. A dissection of this nerve in the species of hagfish studied shows that it takes a course down the sides of the body, the right and left
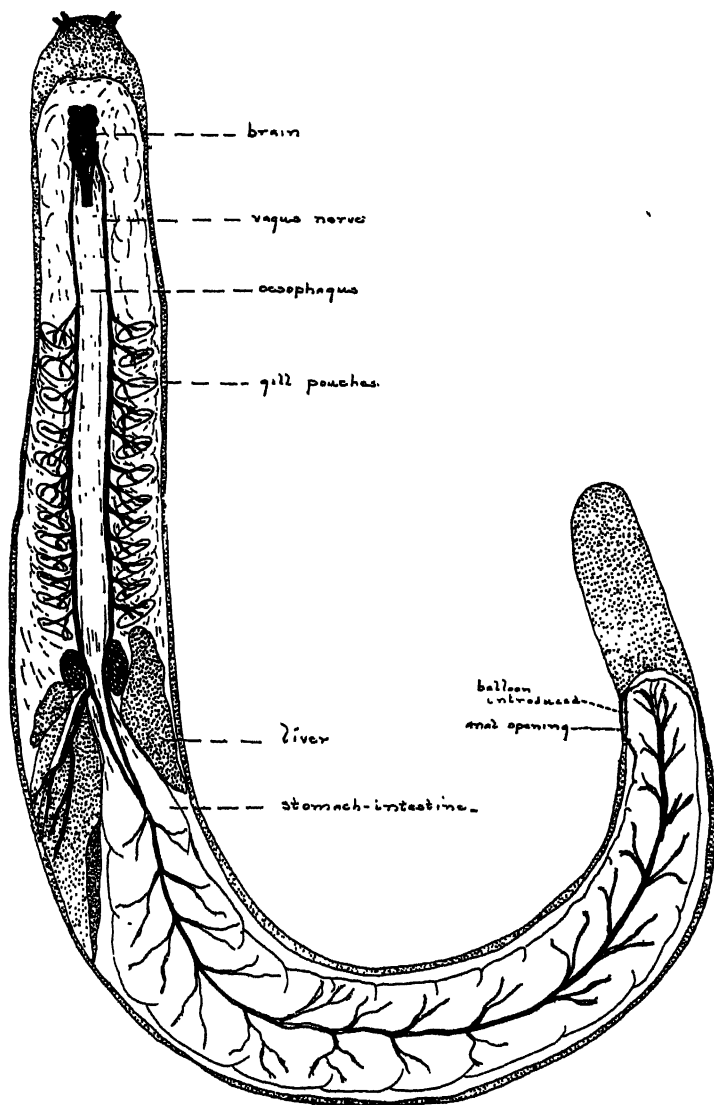
Fig. 22.—Dissection of vagus nerve in the hagfish, with its distribution to the gill sacs, cardia, and stomach-intestine.

nerve trunks joining just over the cardia, whence it passes down the dorsal mid-line of the stomach-intestine to the end of the rectum (Fig. 22). In this drawing the vertebral column and spinal cord have been removed with the dorsal muscles. Furthermore, the dissection revealed that the twelfth gill opening (thirteenth in some animals having thirteen pairs of gill openings) on the left side was greatly enlarged and led directly into the lower end of the esophagus (not shown in figure). This opening proved to be of sufficient size for the introduction of the balloon into the stomach and was most fortunately located for this particular type of investigation. However, the introduction of the balloon, either through the twelfth gill opening or through the anal opening, failed to give anything but negative results. In this particular connection the writer felt that there might be a relationship between the gastric motor

FIG. 23.—A, introduction of dual balloon into the stomach of the hagfish by the gill-anal route, with the rubber t u b e s extending through the respective openings to the recording water manometers. B, dual balloon, showing larger balloon for stomach and smaller one for lower end of the esophagus.

mechanism of this form and that of *Necturus*, in which there was a reversal of the vagus action on the stomach (*178*). Therefore, a series of acute experiments was begun by Patterson and Fair (*184*) on the California hagfish, similar to those conducted on *Necturus*, with the difference that a double balloon was used—a small one in the lower end of the esophagus and a larger one in the stomach proper (Fig. 23 B). These balloons, although in series, were so constructed that there was no air transmission between them. For the introduction of the balloon into the animal's stomach a small piece of glass rod about one-quarter of an inch in length, with rounded ends, was inserted into the open end of the rubber tube coming from the deflated large balloon. This was then introduced through the large gill opening on the left side, gradually worked through the cardia into the stomach-intestine, and withdrawn through the anal opening. With the two balloons in place, the tubes were connected with their respective manometers and inflated (Fig. 23 A). Then, with

the vagi isolated for stimulation, any changes in the cardia or stomach could be recorded upon stimulation of the nerve.

By this gill-anal method which was possible in such an animal as the hagfish, possessing a straight alimentary tract, it was found upon stimulation of either vagus that the cardia contracted while, at the same time, the stomach-intestine relaxed (Fig. 24). There was also a definite contraction of the gill sacs, resulting from this nerve stimulation, as well as some indication that the spinal nerves exerted a motor action on the stomach-intestine of this animal. These results show that the vagus nerve is motor to the cardia and inhibitory to the stomach-intestine, which places this animal in respect to its gastro-vagus action in the same category with *Necturus*, in which the vagus is inhibitory to the stomach.

Turnbull (*228*) and Dahlgren (*63*), in a histological study of the intestine of *Myxine*, the Atlantic species of hagfish, found little or no muscular tissue in its wall. These investigators came to the conclusion, as an assumption from their work on dead tissue, that the peristalsis was carried on by the muscles of the body wall. "In order that this may be possible, the small digestive tube is padded with a layer of large-celled connective tissue, kept expanded by turgidity. These connective tissue cells increase the diameter of the intestine so that it almost fills the body cavity and so brings the intestinal walls close enough to the body wall that the peristaltic action of the latter may be transmitted to the former." Olcott (*158, 159, 63*), in a series of experiments on the live material, has been able to demonstrate that the stomach of this animal possesses the power to contract, and he has graphically recorded on a slowly moving drum the contractions which were doubtless produced by the circular fibers. True peristalsis was also observed when a piece of the stomach wall was placed in a salt solution for one minute and then transferred to a Ringer's solution. This is in agreement with the results on the California hagfish since the stomach is comparatively thin and the muscular tissue correspondingly diminished, accounting for the small contraction curves (Fig. 24). However, since the peristaltic action is quite weak and the walls of the stomach-intestine are seemingly weak and flabby, it is possible that the actual downward movement of the food is not the chief function of the muscle of the stomach wall. Since the straight intestinal tube lies very close to the body wall, which is heavily muscled and capable of great activity, it is possible that the body wall may considerably aid in the process of peristalsis.

PISCES

DOGFISH (*Squalus californicus*)

The digestive tract of elasmobranch fishes has been studied quite extensively both from the histological and from the physiological standpoint and Sullivan (*213*) has given a good review of the more general prin-
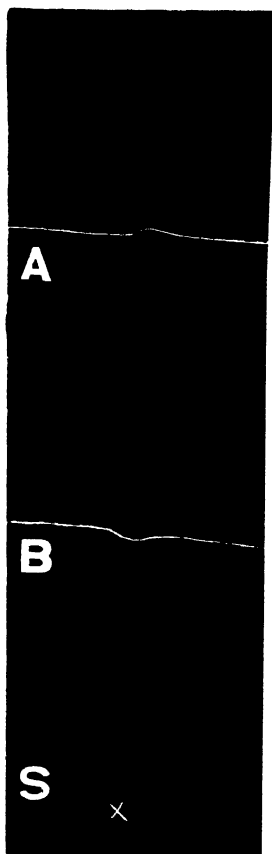
FIG. 24.—R e a c t i o n of cardia, A, and stomach-intestine, B, of hagfish to vagus stimulation. Registration by dual balloon through gill and anal openings. Vagus is motor to cardia and inhibitory to the stomach-intestine. S, signal.

ciples of the subject. A study of the literature concerning the innervation of the stomach and intestine in mammals, and the effect of adrenalin, reveals much confusion and contradictions, and the motor effects of sympathetic stimulation and adrenalin on the stomach of elasmobranch fishes offers another exception to this common view.

Bottazzi (*19*) and Müller and Liljestrand (*154*) were unable to obtain inhibitory effects on the stomach of elasmobranch fishes by stimulat-

ing the anterior splanchnic nerves, but instead got marked activity. The visceral nervous system in these fishes also has other peculiarities, namely, a lack of accelerator (sympathetic) nerves to the heart (*19, 154, 127*) and an inhibitory action of adrenalin on the heart. Lutz (*127*), working on the dogfish, *Squalus acanthias,* and the skates, *Raia erinacea* and *Raia diaphanes,* found that adrenalin caused a rise in tone and an increase in motility of all parts of the stomach, while an extract of the chromaphil bodies had a similar effect although other tissue extracts used for controls were ineffective. Faradic stimulation of the first sympathetic ganglion (gastric ganglion), and of the anterior splanchnic nerves, produced extensive contractions of the stomach. Similar stimulation of the vagus gave moderate contractions with no indication of any inhibitory effect. Furthermore, simultaneous vagus stimulation did not alter the response from the splanchnic nerves. Adrenalin and extract of chromaphil tissue caused a marked decrease in tone and in inhibition of motility of the posterior end of the intestine and the rectum, while faradic stimulation of the posterior splanchnic nerves led to a vigorous contraction of these parts.

Alvarez (*6*) studied peristalsis in the dogfish and ray and found that the cardiac portion of the stomach exhibited peristaltic waves, tonal changes and small rapid contraction waves, while in the pyloric portion which is very different in structure from the cardiac, contraction waves occurred, but no true peristalsis. Furthermore, the dogfish can vomit, but the stomach is unable to empty itself by its own contraction. In the valve gut the movements are slight in the dogfish and absent in the ray. Dobreff (*69*), working on the gastric secretion in sharks found that it was present throughout life, commencing in embryonic life and lasting until death. This worker found that the maximal gastric secretion was reached a few days after the beginning of starvation and that the shark could fast for long periods (112 days), losing during this period about one-third of its body weight. Smallwood (*214*) made a similar observation on the dogfish, *Amia calva,* and found that it was able to live for at least twenty months in an aquarium tank without food, the body energy during this period being derived from the body muscles.

A member of the true fishes, the California shark or dogfish was selected as being a suitable species for the investigational type of work in question. The animal was anesthetized in a solution of two per cent. ether in sea-water, according to the method used on *Necturus,* but in this case a gastrostomy was performed. The best location for the fistula was found to be on the ventral surface, the line of incision not to be over one-

quarter of an inch to the left of the median line extending from the inner ventral base of the pectoral fin caudalward, so as to avoid the lateral vein. At the present time, the work has not proceeded to the point where much can be said in regard to the gastric activity of the stomach of the dogfish. There is, however, good evidence of gastric motor phenomena, the details of which will require additional work to confirm.

<div style="text-align:center">

AMPHIBIA

NECTURUS (*Necturus maculatus*)

</div>

On the completion of considerable work on the frog it seemed desirable to extend the investigation to *Necturus,* a member of that group of aquatic amphibians which is probably the oldest of the present day urodeles (*219*), to determine whether or not the physiological activity and control of the gastric motor mechanism discovered in bullfrogs is the same or similar in this animal.

The general method of study was at first similar to that employed on the bullfrog (*168, 169*), modified to meet the anatomical peculiarities of this type of animal. The animals were anesthetized in a solution of two per cent. ether in water after the method of Sulima (*217*) and a stomostomy was made. This method was found to be unsatisfactory and although the animals lived indefinitely following the operation they invariably died after the introduction of the balloon tube through the stomostomy opening in the floor of the mouth. For example, if the balloon and tube were left in position overnight, the animals were usually found dead in the morning. The presence of the tube in the opening apparently interfered with the normal respiration, thus allowing the passage into the mouth of water which could not be properly expelled through the gill slits; or, because of this abnormal condition the animals may have drowned, since water was found in most cases either in the lung sacs or in the stomach and upper portion of the intestine. No results were obtained by this method and it was discarded. A gastric fistula made in the midline of the ventral surface of the body was also unsatisfactory. The tissues were not sufficiently strong to hold the sutures for any length of time and they were soon torn out by the swimming activity of the animal. This also happened if the abdominal muscles were quickly contracted, resulting in a protrusion of more or less of the visceral mass. An esophageal fistula made about 0.5 cm. to the left of the mid-line, and posterior to the fore limb on the ventro-lateral surface, proved to be more satisfactory. By this method fairly good results were obtained from

about one-third of the experimental animals, but unfortunately the greater majority died of rupture, as in the case of the gastrostomized animals, before results could be obtained from them. However, such a fistula made in the extreme lower end of the esophagus was much more satisfactory than a similar one made in the mid-line, since due to the
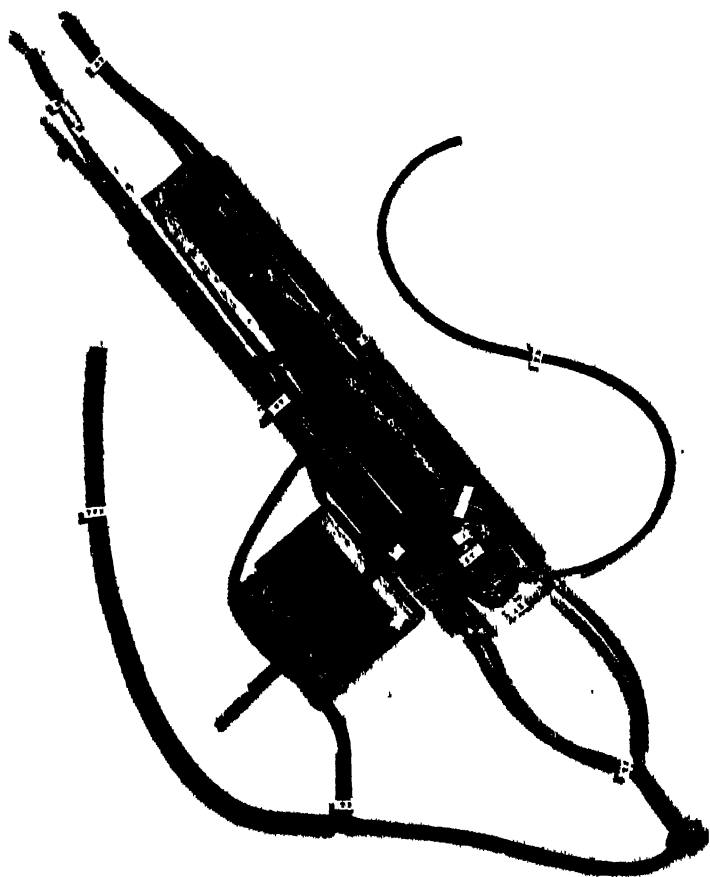
FIG. 25.— This figure illustrates arrangement of apparatus for determining the influence of the vago-sympathetics on gastric activity in *Necturus*. TWF, rubber tube from water faucet; TT, glass T-tubes; WT, water-troughs for lower portion of gills; AH, animal-holder; OT, outlet tubes; TM, tube to manometer with balloon attached at opposite end, the latter being introduced into the stomach through a stomostomy opening in the floor of the mouth (not shown); CTTG, curved T-tube to keep upper portion of gills moist; IV, incisions for vagi; ITC, incision for transecting cord; Th, thermometer; L, ligatures attached to vago-sympathetics; S, support for apparatus; C, clamp to regulate flow of water through tubes.

retaining of the visceral membrane which is attached to the inner sur-
face of the abdominal wall along the mid-line, there was less tendency to
rupture. This sustaining membrane holds back the viscera of the right
side, and especially the large liver, thereby reducing the intra-abdominal
pressure on the tissues directly involved in the making of the fistula, and
in this manner somewhat lessening the possibility of rupture. Simply
an attempt to introduce the balloon into the stomach of a properly pre-
pared animal often results in rupture if the animal becomes excited and
swims about in the water. The animals during the period of experimenta-
tion were kept in water in a darkened tank and in a reasonably cool room.
Because of the disadvantages involved in this method, and other factors
of an apparently inhibitory nature, which will be discussed later, it was
thought desirable to initiate a series of acute experiments on this animal.

In these experiments the method consisted of transecting the spinal
cord between the first and second cervical vertebra under ether anesthesia,
followed immediately by a stomostomy operation for the introduction
of the rubber balloon into the stomach through the mouth and esophagus,
for the graphic registration of the gastric contractions. The animal was
then placed on an inclined board so that the gills floated in the two per
cent. ether and water solution and the vagi were isolated dorsally at their
exit from the skull for a distance of 3 to 5 mm. through incisions about
one cm. to the right and left of the median line ; lifting ligatures were
placed under each nerve. These nerves can be isolated without hem-
orrhage. The incisions were plugged with cotton moistened with normal
saline and the animals were then placed in a normal horizontal position
on a specially constructed animal holder provided with water-troughs, and
the gills were constantly covered with running water, both from above
and below (Fig. 25). In these animals the respiration and circulation
are maintained fairly normal for periods ranging from three to five
days and they may live for periods as long as eight days. During this time
the gastric motility, as well as the influence of the vagi on the empty
stomach, may be studied.

THE MOVEMENTS OF THE EMPTY STOMACH AND THEIR INHIBITION

The recorded observations of the activity of the empty stomach of
Necturus by the esophageal-fistula method are, with some exceptions,
similar to those recorded from the empty stomach of the bullfrog. The
contractions, although somewhat weaker and of shorter duration, re-
semble in character those of the bullfrog but the intervals between the

individual contractions are from five to nine times longer. Likewise, no changes in gastric tonus occur in these fasting animals and for this reason only one type of hunger contraction is exhibited, since the type of these contractions is thought to be primarily dependent upon the degree of tonus under which the gastric mechanism maintains itself at different times (*204*). Under an environmental temperature of about 18°C., which has proven to be the most favorable for maximal gastric activity in this animal, the contractions show an average duration of about forty-five seconds, and the intervals between the contractions vary from one and one-third to five minutes. The form of the contraction is rather slow and the curve is perfectly smooth, showing no smaller superimposed waves. Furthermore, there is no indication that these contractions fall into groups separated by intervals of relative quiescence; they are practically continuous and show a definite regularity which continues for hours, at least after the contractions have once started following the preliminary steps of the introduction of the balloon into the stomach. Such procedure may result in total absence of any gastric activity for several hours and when the contractions actually do start they are very, very feeble at first, but show a definite regularity. They gradually increase in strength until they reach their maximum, which may require from one to three or four hours. Weak acid or alkali of the usual strength, when introduced directly into the stomach, produces temporary gastric inhibition, as do body movements. From one animal a continuous record of the gastric activity of the empty stomach was recorded for seventeen and three-quarters hours in which no periodicity was exhibited, the contractions being regular and continuous. They would doubtless have gone on indefinitely under the conditions had not the temperature toward the end of this period been very gradually reduced by the addition of small pieces of ice to the water in the tank. This reduction in temperature produced a gradual slowing and weakening of the contractions until finally there was a complete cessation of all gastric activity at 7°C. This is a somewhat lower temperature than that required in the bullfrog to produce gastric standstill—on an average, 13°C. This was the only animal on which the influence of temperature was studied.

Upon recovery the animal showed feeble contractions which increased in intensity but they never quite returned to the normal strength of the contractions before the reduction of temperature. It should be borne in mind, however, that this particular experiment was carried out in the month of January while the similar and more extensive experiments on

bullfrogs were carried out during the month of August; this might account, in whole or in part, for the difference in temperature at which the stomachs of the two animals ceased their activity.

During the graphic registration of the gastric activity in *Necturus* it was found that handling or touching the head, and more especially the gills, usually resulted in producing temporary gastric inhibition and this, coupled with the fact that it required such a long time for the contractions to start after the introduction of the balloon into the stomach, might indicate that the gastric mechanism in this animal is under the inhibitory control of a medullary center.

THE INFLUENCE OF THE VAGI ON THE GASTRIC MOTILITY

After the operative procedure necessary in preparing the animals for these acute experiments and the introduction of the balloon into the stomach, there is usually a period of several hours before there is any indication of gastric motility. Finally, weak contractions appear, which gradually increase in amplitude to a maximum. These contractions, on the whole, are practically identical with those obtained by the esophageal-fistula method. A previous report of the author (*174*) indicated that the controlling influence of the vagi on the movements of the empty stomach of *Necturus* was largely inhibitory. In this animal Fischer (*79*) Drüner (*72*) and Norris and Buckley (*157*) have described a glossopharyngeal-vagus nerve complex formed by three branchial nerves. The glossopharyngeal or first branchial nerve shows characteristic pharyngeal, pretrematic and posttrematic rami and sends a general cutaneous and motor branch that anastomoses with the second branchial nerve. The second branchial nerve (vagus 1) has well-developed pharyngeal, pretrematic and post-trematic rami and sends one motor and general cutaneous branch to supply the levator and depressor muscles of the first gill and the over-lying skin which receives an anastomosis from the ninth nerve; other branches supply the levator and depressor muscles of the second gill; an anastomosis occurs with the third branchial nerve forming the innervation of the levator and depressor muscles of the third gill. The third branchial nerve (vagus 2) is very much reduced but pretrematic and posttrematic rami of communis fibers only may be recognized, while the main part of the nerve forms an anastomosis with a branch of the second branchial nerve already mentioned. The ramus intestino-accessorius of the vagus divides into three typical branches: r. lateralis ventralis, r.

intestinalis recurrens, and r. intestinalis, the last of which supplies the lungs, stomach and intestine. While the apparent close linking together of the respiratory and gastric organs might almost lead one to believe that in *Necturus* they were both under the control of a single medullary center, it is more likely that separate centers exist and that reflex stimulation results. However, it is evident that this close relationship between the nerve supply of the gills and the stomach might be materially influenced by conditions affecting respiratory function which might be transmitted to the gastric mechanism reflexly through this glossopharyngeal-vagus complex, and the experimental results of the investigation tend to support this
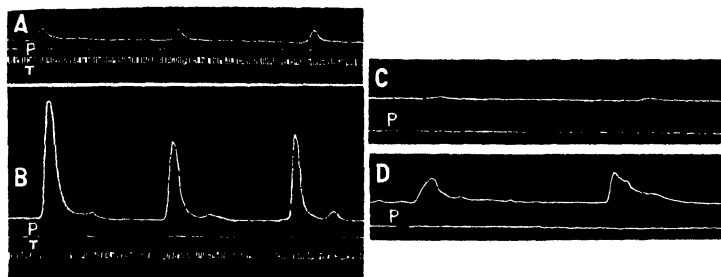
FIG. 26.—Movements of the empty stomach of *Necturus* before and after double vagotomy. A, normal contractions with the vagi nerves intact; B, contractions from the same animal's stomach after section of both vagi. Note the augmentation of the contractions due to the removal of the inhibitory influence. C, indicates how shallow the normal contractions may be in some animals, followed in D by the usual augmentation after double vagotomy. P=0 mm. pressure of water manometer. T, time in 5 second intervals.

belief. Stimulation of the gills with a glass seeker or with forceps usually leads to reflex inhibition of the empty stomach, with cessation of gill movements during the period of the excitation. The afferent impulses arising from gill stimulation pass along the branchial nerves to the vagus center in the medulla, whence inhibitory influence is transmitted down the vagus trunk and along the r. intestinalis to the stomach. Section of the branchial nerves abolishes the reflex effects of gill stimulation. Destruction of the medulla, or section of the vagi, produces a similar effect.

The ligaturing and sectioning of both vagi first produce inhibition of the gastric movements, due to the mechanical stimulation, followed in a short time by the return of the gastric contractions in augmented form, the augmentation even greatly exceeding the amplitude of the normal contractions with the nerves intact (Fig. 26 A, B, C and D). Electrical stimulation of the vagus or even slight traction on either the sectioned or the unsectioned nerve, when the stomach is exhibiting motor activity, will

produce almost immediate inhibition or stoppage of the movements of the empty stomach (Fig. 27 A). This inhibition is of rather prolonged duration, lasting from 30 to 45 minutes or more, depending upon the intensity of the stimulation, and is followed by a gradual return to normal. The effect is the same whether rapidly or slowly induced shocks are used, but the duration of the inhibition is usually longer following stimulation by rapidly induced electric shocks. Cardiac inhibitions also result from electrical stimulation of this nerve. No motor effects have ever been observed from vagus stimulation. These findings tend to show that the fibers contained in this nerve and destined for the stomach of *Necturus* are predominantly, if not exclusively, inhibitory. This pre-

FIG. 27.—Inhibition of the movements of the empty stomach of *Necturus*. A, same animal as in Fig. 26 A and B. At x, weak tetanizing current applied to peripheral end of left vagus after double vagotomy, producing inhibition directly. B, same animal as in Fig. 26 C and D. At x, moderate traction on central end of right vagus after unilateral vagotomy, producing inhibition reflexly. P=0 mm pressure of water manometer. T, time in 5 second intervals

dominant inhibitory action of the vagus on the stomach of *Necturus* is not in accord with the results of other workers on the stomachs of higher animals, since it is now generally conceded that the vagi contain both motor and inhibitory fibers to the stomach, with a predominance of the former. However, the work of Hopf (*94*) on the frog, and that of Bercovitz and Rogers (*13*) on the turtle, while supporting the above statement, seem to indicate that there is some slight increase in the proportionate number of inhibitory fibers present in the vagi to the stomachs of these animals as compared to the number existing in the same nerve of that of higher animals. Furthermore, Carlson and Luckhardt (*55*), have demonstrated that the vagus nerve is inhibitory to the esophagus of the turtle. To the lungs, which must be considered as diverticula of the esophagus, it is predominantly, if not exclusively, motor in the turtle (*54*). Likewise, in the frog it is predominantly inhibitory but also partly

motor to the lungs (*53, 172, 173*) ; while in salamanders, including *Necturus,* it appears to be exclusively inhibitory (*126*).

Stimulation of the central end of the vagus after unilateral vagotomy, either with induced electric shocks or by traction, leads to a reflex inhibition of the movements of the empty stomach (Fig. 27 B). However, following bilateral vagotomy the reflex is entirely abolished, showing the reflex pathway to be through the vagus. This reflex activity on the gastric motor mechanism of *Necturus,* as exhibited by central stimulation of the vagus and in most cases by stimulation of the gills in the intact animal, is in accord with the results of other investigators on the reflex inhibition of certain internal organs in other animals. McWilliam (*142*), working on the reflex excitation of the cardiac nerves of the eel, showed that various types of slight stimulation of either gill caused a sudden and powerful inhibition of the heart, of considerable duration (half a minute), after the discontinuance of the gill stimulus. Stimulation of the gill apertures, the interior surface of the branchial chamber, the skin of the head, and that of the tail, are also effective in producing cardiac inhibition. Cardiac inhibition may also be obtained in the carp, perch, rudd, etc., as in the eel. Goltz (*85*) also found that various types of stimulation applied to different parts of the frog's skin led to an increased hypertonus and motility of the stomach, and these observations were confirmed by Contejean (*58*) and Steinach (*215*). Meltzer and Auer (*145*) showed that the vagus contains inhibitory fibers to the cardia of the rabbit, which may be excited reflexly by stimulation of the central end of the remaining vagus. Von Openchowski (*234, 235*) reports that, with the vagi intact, reflex dilatation of the cardia may be induced by stimulation of the sciatic nerve and various internal organs, while Luckhardt and Carlson (*125*) by gentle mechanical stimulation applied to the skin of the mandible, gills or front legs of the axolotl, induced lung contractions of reflex origin. Such reflex action from electrical or mechanical stimulation of cutaneous nerves was not obtainable, however, in *Necturus*. In the curarized *Cryptobranchus,* stimulation of cutaneous and visceral sensory nerves causes, in most cases, reflex lung contraction and reflex cardiac inhibition (*126*).

In four animals the brain was exposed dorsally and the rootlets forming the glossopharyngeal-vagus complex were isolated, with a portion of the brain. Upon electrical, or slight mechanical (traction), stimulation, motor effects were observed in one animal in both the stomach and the gills. The motor response in the stomach appeared either in the form of one or two weak contractions without inhibition or the contractions were followed by inhibition. However, in the rest of the animals so

studied only inhibitory effects were observed on the stomach, while motor effects occurred in the gills. This would possibly suggest the presence of a few motor fibers in the vagus for the stomach of *Necturus* but it must be granted that if such motor fibres do actually exist, they must be extremely in the minority. In other words, the predominance of the inhibitory fibers in the vagi is apparently in inverse order to the arrangement of these fibres as found in the same nerve in other animals. In a few experiments an attempt was made to stimulate the splanchnic nerve fibers supplying the stomach after laparotomy. Rapidly induced electric shocks were used. Out of four such animals three gave positive and one negative results. In those stomachs in which peristaltic activity was exhibited the contractions started in the upper third and advanced slowly toward the pylorus but none of the waves was observed to pass over the pylorus. In two animals the peristaltic contractions resulting from the stimulation were so strong at times as completely to obliterate the lumen of the stomach. In the other animals the contractions were weak. Several contractions may be obtained from the same stomach by repeating the stimuli, but the contractions gradually become weaker until finally they cease altogether. Therefore, the experimental evidence for the existence of motor excitatory fibers via splanchnics to the stomach is much more pronounced than for the presence of such fibers via vagi in *Necturus.*

The results here presented on the inhibitory influence of the vagi on the stomach of *Necturus,* together with certain inhibitory phenomena presented in the literature on the esophagus of the turtle, the hearts of fishes and the lungs of frogs, *Necturi,* and other salamanders, indicate that this inhibitory innervation via vagus plays an essential rôle in the motor activity of the gastric mechanism. This gastric inhibitory action probably does not arise through the action of the sympathetic fibers that might join the vagal trunk, since the stimulation of the vagus invariably produces inhibition which would tend to rule out this factor as being of any importance. However, the experimental results *in toto* on one species cannot be transferred to another species, because of the evident variations in the degree of the primitive motor control retained in the anterior portion of the gut in different animal groups.

To summarize: The contractions of the empty stomach of *Necturus maculatus* are practically continuous like those of the bullfrog, but the individual contractions are weaker and the intervals of rest are much longer. No changes in gastric tonus were observed. Weak acid or alkali, when introduced directly into the empty stomach, produces temporary in-

hibition. Body movements of the animal also cause a similar effect. Bilateral vagotomy, after a prolonged period of gastric inhibition, leads to a marked augmentation of the normal contractions by removing the inhibitory influence on the stomach. Electrical stimulation of the vagus, or even slight traction on either the sectioned or the unsectioned nerve when the stomach is exhibiting motor activity, results in almost an immediate inhibition of its movements. Stimulation of the central end of a vagus after unilateral vagotomy, either with induced electric shocks or by traction, causes an inhibition of the movements of the empty stomach reflexly, the nerve pathway being via intact vagus nerve since bilateral vagotomy abolishes the reflex. It is also possible to obtain a similar reflex on the stomach from stimulation of the gills with the vagi intact. The inhibitory influence of the vagi on the stomach of *Necturus* is predominantly, if not exclusively, inhibitory, and it therefore plays an essential rôle in the motor activity of the gastric mechanism. It is also probable that the splanchnic nerves supply motor excitatory fibres to the stomach.

FROG (*Rana catesbiana*)

It is now evident from the more recent work of Cannon (*35*), Cannon and Washburn (*39*), and Carlson (*41*), that the sensation of hunger is caused by contractions of the stomach wall in contra-distinction to the older hypotheses in existence; e. g., the theory that hunger is a general bodily sensation, that it is due merely to emptiness of the stomach, that it arises from hydrochloric acid in the empty stomach, and lastly, that it is due to turgescence of the gastric glands—"turgescence theory" of Beaumont. Notwithstanding the large amount of literature upon the movements of the gastric motor mechanism, little has been done to establish the exact analogy of the gastric hunger contractions throughout the vertebrate series. Certain facts have been ascertained regarding the state of the fasting stomach in higher animals, and certain inferences have been drawn from these facts, but since the complex functions of man are unravelled many times from a study of lower forms it is of some physiological importance to have a series of similar investigations conducted on the remaining classes of the vertebrates and even perhaps upon certain forms of the invertebrates. Up to the year 1916, however, all the principal work had been done on a single animal group, the mammalia, with the exception of a little uncompleted work on the group of the aves.

The extensive studies of the author (*168, 169, 170, 171*) on the gastric motor mechanism of the bullfrog has extended our knowledge considerably in the field of gastric physiology, and especially in comparative phys-

iology, which is always so important in giving us clues to unravel the more complex mechanisms of physiologic behavior in man.

Various investigators have worked with the spontaneous movements of the gastro-neuro-muscular apparatus of poikilothermic animals, studies which have been confined principally to the frog under varying conditions. They have studied the excitatory and the inhibitory influences upon gastric motility, through its extrinsic innervation by means of electrical, mechanical and chemical stimuli, as well as the direct effects on this organ. With regard to the gastro-inhibitory effect of the vagus certain experiments upon the frog are of special interest. Volkmann (232), in 1841, found that if the medulla oblongata is destroyed or the vagi are cut, a lively peristaltic movement in the stomach is observed. Goltz (85), in 1872, confirmed the above results, but neither of these authors was able correctly to interpret his findings; the former could not yet think of inhibition, and the latter, although the interpretation suggested itself, could not conceive of the idea that inhibitory and motor-nerve fibers could be contained in the same nerve trunk. The appearance of a movement after the section of the vagi, in a stomach previously at rest, seems to indicate that in a normal state these nerves exert an inhibitory influence upon the stomach.

The results obtained by Goltz (86) from curarized frogs which had been left unfed for some days previous to the beginning of the experiment showed, in addition, that the automatic movements of the frog's stomach disappeared after the destruction of the brain and cord, as well as after the cutting of both vagi. According to this observation the vagi would contain inhibitory fibers for the stomach but, since the gastric wall remained in a more or less tonic condition and was not followed by expansion as far as I am able to determine from a review of Goltz's paper, the movements of the frog's stomach itself must have been suppressed by the artificial excitement of the vagi. Furthermore, he states that the mere cutting of the vagus with scissors in close proximity to the esophagus gives rise to violent movements in the wall of the stomach. This would indicate the existence of motor fibers for the frog's stomach.

The presence of gastro-inhibitory fibers in the vagi have been conclusively shown by Langley (117), Meltzer (144), May (133), and Cannon (31), in mammals. According to Kronecker and Meltzer (114), the tonus of the cardia for the rabbit at least is diminished or inhibited at the onset of each deglutition, and if many deglutitions follow one another in rapid succession, the tonus may be entirely abolished. This relaxation of the cardia is of central nervous origin since it takes place even

when the esophagus is severed, but disappears when the vagi are cut. Auer (*8*) has reported that only a slight degree of reflex inhibition of the stomach is obtained through the vagi in rabbits. Von Openchowski (*233*) has described nerve twigs of the vagi in the proximity of the cardia, from one of which he obtained by stimulation contraction, and from another relaxation of the cardia. According to May (*132, 133*), the vagi contain both motor and inhibitory fibers for the stomach musculature. Stimulation of the vagus produces two effects, namely, an inhibitory or dilatory effect followed by an increase of gastric muscular tone and movements, the former predominating in the cardiac end of the stomach and the latter in the pyloric end. Similar effects were produced by "anemia" of the stomach when it was suddenly produced. This author also believed that the splanchnics had no direct influence, either motor or inhibitory, on the stomach muscular wall. Later investigations by Cannon and Murphy (*38*), and Auer (*8*), have shown that the inhibition of the gastric movements of digestion is produced through the splanchnic nerves and the same has been verified by Carlson (*44, 45*) for the gastric hunger contractions.

Furthermore, it has been shown by Cannon (*30*) for the digestive movements and by Carlson (*44, 45*) for the hunger movements that the gastric tonus is largely maintained through the vagi. Mayer (*134*) has described three motor effects resulting from vagus excitation in the neck of rabbits, namely: (*a*) the cardial part of the stomach becomes very stiff, then follows a subsequent contraction—pyloric wave. (*b*) The usually observed depression between the cardial and pyloric portions becomes more manifest and depressions in other parts are noted. (*c*) The whole stomach musculature passes into a state of tetanic contraction which persists a long time. Longet (*131*) did not obtain such results from vagus excitation in the neck of this animal. The discrepancy in the results was due to the fact that in the period of digestion the above mentioned effect of the nerve action is not manifested. Adrian (*1*) verified, by electric excitation of the plexus coeliacus and its neighborhood, movements in the cardia and pylorus.

The experimental work in connection with the excitatory and inhibitory movements of the frog's stomach has not been confined alone to the vagus. Various other nerves under stimulation have been found to exert a marked influence on the gastric motor mechanism. Waters (*237*) noticed that strong stimulation of the third, fourth, fifth and sixth nerves in the frog at their exit from the spinal cord led to contractions of the stomach, as well as of the esophagus and sometimes of the small intestine. Steinach

and Wiener (*216*) have described motor effects in the frog's viscera as a result of stimulation of the posterior roots. According to these authors the stomach is innervated from the third, fourth and fifth spinal nerves. Dixon (*68*) verified the above results by stimulation of the rami communicantes of the third, fourth and fifth spinal nerves, which corresponds to the origin from the spinal nerves described by Waters, and Steinach and Wiener. According to this author stimulation of the rami communicantes of the fourth spinal nerve produces tonic contraction together with augmented and more regular automatic stomach contractions. Stimulation of the third and fifth rami produces a similar but smaller effect. The vagus contains inhibitory fibers to tonus but upon excitation of this nerve augmented automatic movements usually result, but no increase in gastric tonus is ever observed. Müller and Liljestrand (*154*) found the sympathetic division to activate the stomach of the frog. Furthermore, Contejean (*59*), in studying the innervation of the stomach of Batrachians, discovered that electrical excitation of the sympathetic caused no relaxation of the gastric reservoir; it even caused contraction, although to a lesser degree than excitation of the vagus. It is with the vagus and not with the sympathetic that this author has been able to provoke arrest phenomena in the peristaltic movements of the stomach. and he thinks the vagus acts especially on the longitudinal fibers while the sympathetic commands the circular fibers although they are probably not absolutely dependent upon the sympathetic. He has also quite regularly provoked contraction of the pylorus in dogs by electrification of the vagus. Meltzer (*143*) learned that very weak excitation, when applied directly to the stomachs of dogs, cats, rabbits and frogs, caused contraction, if the electrode was placed on the outer side of the stomach. This varied somewhat with the animal used, but the main excitatory parts were according to him the pylorus, the cardia, and slightly the fundus, except in the case of the frog in which these points were not definitely localized.

Battelli (*10*) studied the gastric movements under the influence of drugs, and draws the interesting conclusion that the vagus, by the inner branch of the accessorius, not only regulates the moving phases but also the inhibition phases of the stomach muscles. Doyon (*71*) found that excitation of the peripheral end of the vagus, under ordinary conditions in dogs undergoing digestion—the nerve of the opposite side being intact—invariably provoked exaggeration of the stomach movements. But he never observed any clearly marked suspensory action of the nerve on the gastric reservoir, nor a diminution of the gastric tonus. According to this author an injec-

tion of pilocarpine or strichnine appears to favor the putting into play of the inhibitory power of the vagus nerve on the movements of the stomach, since excitation of the peripheral end of this nerve after the injection causes a decontraction of the gastric reservoir, followed by an exceptionally energetic contraction, and he suggests that these substances provoke a combined effect through the gastro-inhibitory and gastro-motor fibers of the vagus. Barbéra (9) used the stomach sack method in investigating the spontaneous activity of the frog's stomach. The brain was separated from the medulla and two cannulas were introduced into the stomach; one into the cardia and held by an esophageal ligature, and the other through the pylorus and fixed by a duodenal ligature. The stomach was then filled with normal saline solution at a small pressure of from 3 to 4 cm. in the ascending cardial orifice and connected with a Marey apparatus for registering the movements or alterations in its internal capacity. With such an arrangement, Barbéra studied the effect of electrical excitation on the gastro-spontaneous movements, and concluded that the stomach muscular movements were reflex movements. Glaessner (84), with a somewhat similar arrangement, studied the effect of different substances (poisons) in the stomach. He used a double cannula, instead of two single cannulas, which he introduced through the esophagus. Dixon (68) undertook a similar inquiry but used an internal pressure of from 10 to 20 cm. up in a frog's stomach. He thought that the optimal water pressure varied greatly with different animals and emphasized the fact that the spontaneous movement with his method exhibited greater regularity.

There were generally differences of opinion among authors as regards the animals. Some thought that regularity and strength of the spontaneous contractions varied according to the animal, and that in the case of frogs, winter frogs were not suitable. Adverse ideas also existed as regards unfed, and fattened, frogs. Morishima and Fujitani (150) investigated the spontaneous movements of the frog's stomach (Esculenta) with a William's heart apparatus. They isolated the whole stomach *in toto*, but used only the part in the neighborhood of the pylorus, so that when the double-walled cannula was tied in the fundus the prepared "Magensack" constituted about one-third of the whole stomach wall. The pyloric end was closed by a ligature and the whole placed in Ringer's solution into which a slow current of oxygen was led. These authors verified that regular and strong contractions are obtained with well fed frogs, and they do not think that the condition of the stomach—that is, full or empty—is of great consequence. Glaessner (84) used either freshly caught hungry frogs, or those confined a long time, fed on rain-worms, etc., and then left

without food for some days before the experiment. Dixon (*68*) thought that hungry frogs such as Glaessner and others used gave more unsatisfactory results than normal animals, and that if kept in confinement for two months were quite unfit for use. According to Morishima's and Fujitani's experience (*150*), the stomach filled with food is the best for studying spontaneous movements, but in case of frogs kept a long time in confinement better results are obtained if frog-muscle or rain-worms are fed them some days before the experiment. More recently, Hopf (*94*), with an arrangement similar to Barbéra's, has shown conclusively that stimulation of the vagus in the frog can have the effects of inhibition and of excitation on the gastric reservoir. In order to obtain good results the stomach must be placed in a good condition of automatic contraction (motility). The phase of inhibition is then seen preceding that of excitation, and the excitation is stronger than the inhibition, the intensity and the duration of the current having little or no influence on the vagus effect. According to this author there is a great distinction between fed and unfed frogs in the size and stability of the automatic stomach movements, but winter frogs give good results if previously fed.

The comparative studies on the amphibia were made on the bullfrog (*Rana catesbiana*), better known in the fish markets as the "jumbo frog." All the bullfrogs were obtained from the South, Louisiana, through local dealers in Baltimore and Chicago and were stomostomized (Fig. 28) under
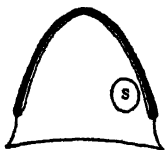
FIG. 28. —Ventral view of frog's head, showing location of stomostomy at S.

ether anesthesia. This simple operation (*169*) consists of making a circular opening on one side between the ramus of the inferior maxillary near the posterior angulosplenial region and the anterior cornua of the hyoid bone through the skin, the submaxillaris (mylohyoideus) muscle, and the lining membrane of the pharyngo-oral cavity (*73*), of sufficient size (about 8 mm. in diameter) to admit the balloon and the attached rubber tube which connects with the recording manometer (Fig. 29). This operation may be bloodlessly performed provided care is taken to avoid injury to the superficial vein (vena maxillaris inferior) which runs along the insertion of the submaxillaris muscle, and turns inward at its hinder border to join the lingual vein. Through this artificial opening or stomostomy, which usually heals in from three to four days so that the animal may be used
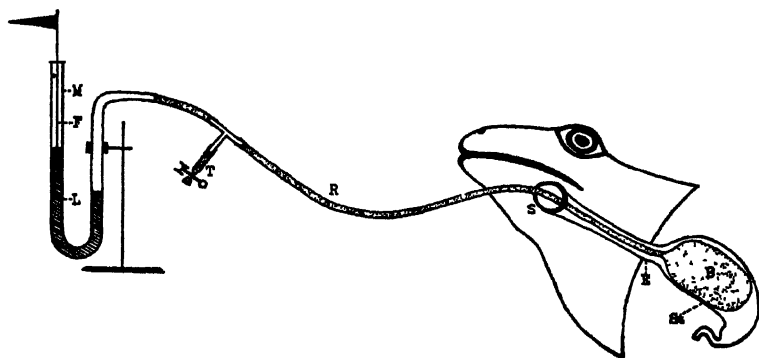
FIG. 29.—Diagram showing method of recording gastric movements of the frog's stomach. B, rubber balloon in stomach; M, manometer; F, cork float with recording flag; L, manometer liquid (water); R, rubber tube connecting balloon with manometer; T, side tube for inflation of stomach balloon; S, stomostomy; E, esophagus; St, stomach.

for experimental tests with normal results, is introduced the delicate rubber balloon by means of a glass seeker. Then by opening the frog's mouth the balloon may be carefully pushed into the stomach with the seeker, through the short esophagus, which may be greatly enlarged. Yet, when empty, it is completely closed by folding of the walls. In this position the balloon may be inflated through a glass T-tube and the desired pressure obtained in the manometer. The rubber tube passing through the stomostomy to which the balloon is attached lies in the posterior part of the pharyngo-oral cavity under the free edge or at the side of the tongue, and thereby eliminates any possibility of the stomach pressure fluctuations on the balloon which are transmitted by air transmission to the surface of the liquid in the manometer, being partially or entirely shut off. This would be the result if the flexible rubber tube passed between the jaws and the animal could bite upon the tube. Like the gastric fistula in dogs there is not much trouble in the way of closing up of the stomostomy as long as the animal is being used daily, but when unused it usually closes up completely in from five to twenty days in the bullfrog. The opening appears to be of practically no inconvenience to the animal. It will have to be admitted that practically all the methods previously used by investigators for studying the spontaneous movements of the frog's stomach were more or less pathological in their entirety, while the method used by the writer allows the animal to remain in a perfectly normal condition at all times, since the stomostomy in the floor of the mouth does not interfere in any way with the normal physiological activity of the gastric motor apparatus or any other system of the body. The large species of frog is also superior

with this method, since more accurate results are usually obtained from larger animals.

During the recording of the gastric hunger movements, the animals were placed individually in small laboratory table sinks, 7 by 10 inches, and 5 inches in depth. The bottoms were covered with several layers of filter paper partially to close the outlet, and water was allowed to drip very slowly from the faucet. Each sink was then covered, with the exception of a very small opening for the passage of the rubber tube from the balloon in the frog's stomach to the manometer. With this arrangement the animals were practically concealed from all disturbing influences and in the sinks, darkened as they were by opaque covers, the animals felt themselves securely hidden and would remain very quiet for long periods of time. Two animals were always used at the same time, the one as a control on the other, and the same tests were always applied to both. For the temperature experiments it was necessary to use different devices. To determine the effects of raising the temperature, upon the movements of the gastric hunger apparatus, the animal was placed in a glass cylinder of 7.5 inches in diameter and 6 inches in height, having a 2.75 inch raised base of wire gauze covered with a circular galvanized iron plate, the size of the interior of the cylinder. The animals stood upon the raised base and occupied the upper 3.25 inches of the cylinder. The top of the cylinder was provided with a wooden cover containing two small openings, one for a thermometer, and the other for the rubber tube from the balloon. Around the glass cylinder was wrapped a dark colored wet towel to darken the interior, and the whole was placed in a large vessel containing water at ordinary room temperature, and rising within about one-half of an inch of the galvanized iron plate within the cylinder. The temperature of the water was now very gradually increased at the rate of about 10°C. per three hours, and continuous records of the hunger movements were recorded. On the other hand, the effects of cooling or lowering the temperature was determined by placing the animal in a box 12 by 10 inches, and 8.5 inches in height, the sides of which were covered with one-quarter inch mesh wire gauze. The top and bottom were of wood. Around the sides and top was placed a dark colored wet towel to darken the interior as in the case of the cylinder above, as well as to shut out all possible disturbing influences. The animal, so arranged, was placed in a refrigerator, the door of which had been previously left open until the temperature of its compartment reached approximately that of the ordinary room temperature. The temperature, obtained by a thermometer in the box, was lowered by the gradual closing of the refrigerator door, at the rate of about 10°C. per

three hours, while continuous records were being taken. However, in one case where it was desired to reduce the temperature to a very low degree, a freezing mixture of cracked ice and salt was packed around the glass cylinders above described and the animals then placed in position and connected with the recording apparatus. As might be expected, this did not give nearly as satisfactory results as did the refrigerator method, since the temperature was reduced too rapidly. However, this very low temperature did bring out certain additional facts of rather great importance, which the other method did not. All the records from the frog were taken on a slowly moving drum revolving at the rate of about fifty minutes per revolution.

THE CHARACTER OF THE MOVEMENTS OF THE EMPTY STOMACH

The recorded observations upon the activity of the gastric hunger mechanism of the frog have numerous points of dissimilarity as compared to the numerous observations already on record for higher animals. Thus, Carlson (46) has demonstrated that the empty stomach, during prolonged fasting, exhibits three types of motor activity, for a description of which the reader is referred to another section of this paper. (See p. 228.)

In the frogs under observation there were no tonus changes observed, not even in prolonged fasting. This would seem to confirm the work of Dixon (68) on the vagus of the frog, namely, that excitation of this nerve causes no increase in gastric tonus although augmented automatic movements usually occur. Since the different types of these hunger contractions are dependent upon the degree of tonus of the stomach, and since there are no tonus changes in the frog's stomach, it would be expected that only one type of hunger contraction would be exhibited by this animal, and this was found to be the case. This particular type of contraction shows an average duration of about one and three-fifths minutes, and the intervals between the contractions vary from sixteen to thirty-three seconds. These contractions are very powerful and are evidently analogous to the thirty-seconds rhythm in man and dog (type I contractions) but the individual contractions are very much more vigorous, that is, if we take into consideration the body weight of the frog as compared to the body weight of the above mentioned animals. In fact, they even excel in strength and amplitude the most powerful contractions from either man or dog in prolonged fasting (Fig. 30). In general appearance the contraction is rather slow, the curve is perfectly smooth and shows no smaller superimposed waves, and there is no indication that the contractions fall into groups, separated by intervals of relative quiescence. In the higher animals the

hunger contractions are periodic and represent simply more vigorous peristaltic movements during which the stomach becomes markedly hyper- tonic (*111, 204*). On the other hand, the gastric hunger contractions of the frog are continuous and show a definite regularity which goes on hour after hour and day after day, with no periods of rest except for the few seconds' pause between each individual contraction. This corroborates the work of Morishima and Fujitani (*150*) on the frog (Esculenta) that
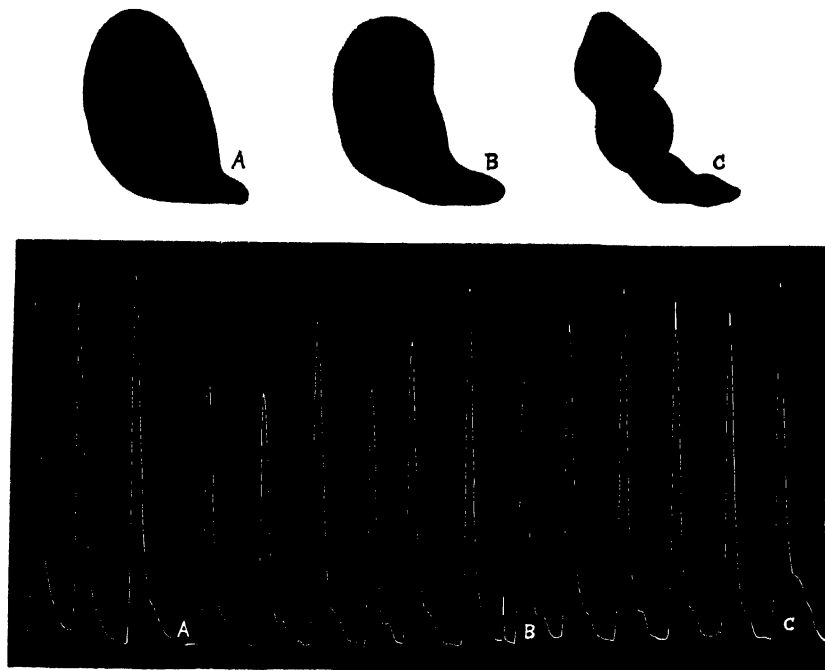
FIG. 30.—Hunger contractions of the frog's stomach after twelve days' fast. A, out- line of stomach (as seen by X-ray and bismuth balloon), between hunger contractions with stomach relaxed. B, outline of stomach at the height of a moderately strong hunger contraction. C, outline of stomach at height of a very strong hunger contraction. Water manometer.

very regular curve tracings may be taken hourly, eventually ten hours, and they have published a series of these normal curves selected at definite intervals which extend over a period of about eight and one-half hours from the beginning of the experiment. This corroboration is all the more valuable, as the method employed by these authors is totally different from the one used by myself. It was also found that when the pressure in the balloon in the frog's stomach was increased, it increased the pressure in the

manometer only momentarily, the stomach simply dilating to accommodate itself to the increased size of the balloon. This may be repeated several times with apparently no change in the contractions or increase in the manometric pressure except temporarily, but finally a limit of stomach expansion will be reached, in which further to increase the pressure by blowing reasonably will be impossible, and at the same time the manometric pressure will be markedly increased. This, no doubt, is an adaptive accommodation which this low form of vertebrate animal possesses, since the periodic habit of feeding is unformed and when food is abundant it eats greedily, the stomach dilating to act as a reservoir for the food.

THE INHIBITION BY ACID AND ALKALI

It is now demonstrated that the tonus and the hunger contractions of the empty stomach in man and dog are temporarily inhibited by mechanical and chemical stimulation of the nerve endings in the mucous membrane of the mouth, in the esophagus, and in the gastric mucosa (*42, 43, 44, 45*). Similar stimulation, when applied to the intestinal mucosa, also produces the effect of gastric inhibition (*26*). This inhibition is initiated by stimulation of nerve endings in the gastric mucosa, and not by mechanical tension or pressure on the stomach wall. The results on normal frogs compare generally with those on man and dog already reported, with some few exceptions. When water, sodium carbonate—1 per cent. solution—and hydrochloric acid—0.5 per cent. solution—are introduced very slowly into the empty stomach of the frog, through a small rubber tube passing through the stomostomy, they invariably produce inhibition varying in degree with the stimulating power of the substance introduced. The duration of the inhibition depends upon the quantity and nature of the material introduced into the stomach and not so much upon the degree of the hunger contractions as in the case of the higher animals, since there are no tonus changes and only one type of contraction exhibited by this animal. In normal frogs 5 to 10 cc. water introduced directly into the stomach through the tube usually produces a weakening of the contractions (Fig. 31 A), but never in any of my experiments have I witnessed complete inhibition of the gastric movements. The partial inhibition is seen to come on very gradually, as is indicated by a lessening in the amplitude of the hunger contractions, which usually extend over a period of from ten to fifteen minutes followed by a gradual recovery to normal. The water so introduced was at ordinary room temperature and should correspond approximately to the temperature of the frog's body; therefore the water in the

stomach must have produced the temporary inhibition through a stimulation of the nerve endings in the gastric mucosa, for an explanation of which the reader is referred to a later section of this paper. (See p. 233.) The in-
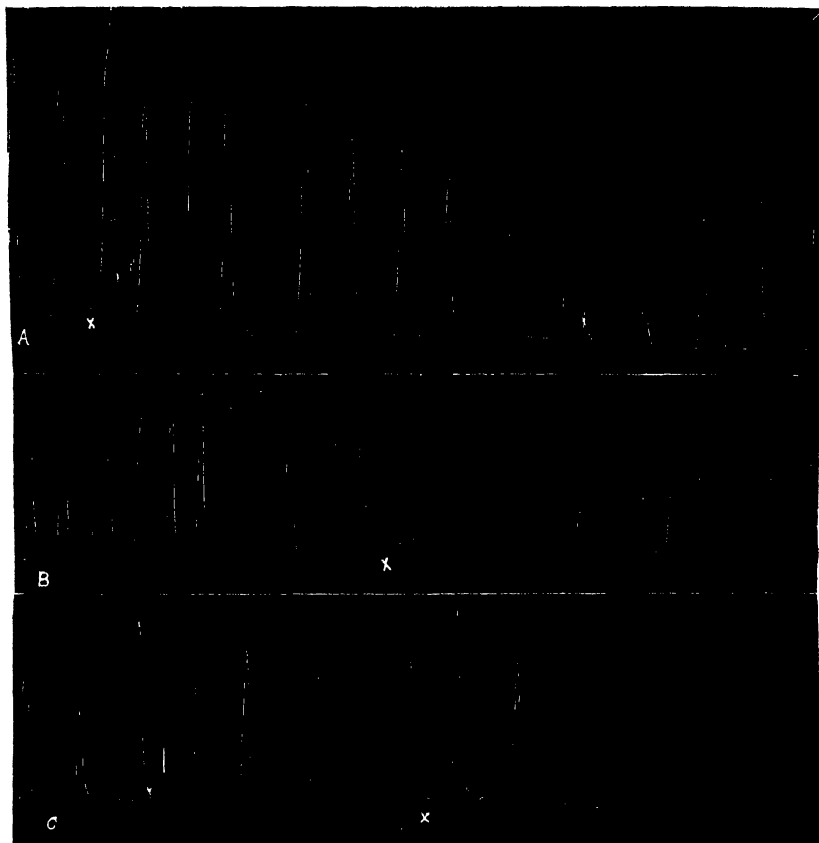
FIG. 31.—Records from the frog's stomach after fourteen days' fast, showing the inhibitory effects produced by different substances when introduced into the stomach. Tracing A : At x 10 cc. water introduced directly into the stomach. (The slight drop in tonus after x was due to bubbles of air escaping through the manometer.) Tracing B : At x 5 cc. of 1 per cent. solution of sodium carbonate introduced directly into the stomach. Tracing C : At x 5 cc. of 0.5 per cent. solution hydrochloric acid introduced directly into the stomach. Water manometer.

troduction of 5 cc. sodium carbonate, 1 per cent. solution, directly into the stomach, produces a more marked inhibitory effect than does the water; the contractions may be greatly weakened or they may be completely inhibited for one and one-half to two minutes (Fig. 31 B). Five cubic centi-

meters hydrochloric acid, 0.5 per cent. solution, causes complete inhibition of the hunger contractions for periods ranging from seventeen to twenty-five minutes (Fig. 31 C). The duration of the inhibition in the case of acids and alkalies seems to be directly proportional to their concentration and the total quantity introduced, always being more marked in the case of the acid. The cessation of the inhibition by these substances probably marks their passage into the intestine, or their fixation and neutralization. The inhibition of the gastric contractions in the frog varies from that of the dog and man in that they are not immediately produced after the introduction of the substance into the stomach. There are usually, however, from one to four or five strong contractions before the inhibition becomes complete. This would seem to indicate that the gastric reflex apparatus of the frog had not reached the high degree of efficiency found in the stomachs of higher animals.

When water, alkali or acid of the above concentration, and in amounts as used for the stomach, were introduced directly into the mouth cavity of the frog through a small rubber tube which barely passed through the stomostomy into the mouth, it was found that the inhibitory effects produced were very slight and perhaps might even have been negative altogether were it not for the fact that some of the solution probably finds its way very soon into the stomach and there may produce inhibition by coming in contact with the gastric mucosa. These observations on the difficulty of inhibiting the hunger movements from the mouth are in agreement with those reported by Rogers (*200*) for the rabbit and by King and Connet (*111*) for the guinea-pig, except that in these two animals the reflex inhibitory mechanism of the stomach from the mucous membrane of the mouth appears to be entirely absent, since these authors have obtained only negative results. The above mentioned substances, when placed into the mouths of higher animals (dog and man), produce a marked inhibition of the gastric hunger movements reflexly. Therefore, it would be reasonable to believe that the cerebral processes are not so highly developed in these animals, the frog included, as in the case of man and the dog. It was impossible to try any of these experiments on the turtles because of the viciousness of these animals. Reflex or psychic inhibition of the hunger contractions in both the frog and the turtle was obtained by showing these animals a small live grass frog on a covered glass plate. This agrees with the results obtained from dogs that the sight or smell of food leads to temporary inhibition of the gastric hunger contractions. Anything which frightens, annoys or angers these animals also leads to temporary inhibition of the contractions.

THE MOVEMENTS OF THE FILLED STOMACH AND THE EMPTYING TIME

In the higher animals (dog and man) there is a marked distinction between the gastric movements in normal digestion and the gastric hunger movements of the empty stomach. Acids in concentrations equal to that of the gastric juice when introduced directly into the stomach do not inhibit the movements of the stomach in digestion but will inhibit the hunger contractions (*43*). In the rabbit (*200*) and in the guinea-pig (*111*) these two types of gastric contractions are less sharply differentiated, although during fasting the stomach activities may be greatly augmented. In the case of the rabbit the inhibitory action of acid'gives the same general results as for the higher animals, with the exception that the effect appears to be less pronounced. In the guinea-pig, according to King and Connet (*111*) acid placed in the stomach gives negative results.

Since the cannibalistic traits of the bullfrog are well known (*66*), it is a very easy matter to obtain these animals with a filled stomach, and furthermore, if the animals are kept in separate compartments, the amount of food can be controlled at any one feeding. The animal when hungry usually captures its prey (small frog) by the anterior portion of the body as soon as it strikes the water, and swallows it alive, and I have several times observed one of these animals to devour as many as four adult grass frogs in as many minutes and have watched with intense interest the struggling of the smaller frogs in the stomach of the larger. At times they would appear to crawl up into the esophagus when it would become necessary for the larger frog to swallow vigorously several times in order to keep them down. However, these animals are soon asphyxiated since the large esophagus is completely closed by foldings of its substance and therefore effectually prevents any accession of air into the stomach. The frogs for the experiments were usually fed two live grass frogs each, and after a period of from thirty minutes to one hour, in order to allow sufficient time for asphyxiation, the balloon was introduced into the stomach and connected with the recording apparatus. Records of the frog shortly after feeding (Fig. 32 A) when compared with the normal hunger records (Fig. 30) show but very little change, if any, from the stomach of the hungry animal. The only observable variation is, perhaps, a very slight increase in the rate of the contractions. This is in confirmation of the view, put forth by Morishima and Fujitani (*150*), that the stomach, full or empty, is not of great consequence as regards the regularity and intensity of the spontaneous movements, although they did not offer sufficient proof to uphold their hypothesis. These facts contradict the ideas of Hopf (*94*),

who claims that there is a great distinction between fed and unfed frogs in the size and stability of the automatic stomach movements, and it is probable that the method which he employed was partly at fault, and pathological.

The question arose in respect to how long it required for the stomach to empty itself after feeding. This was determined after feeding the
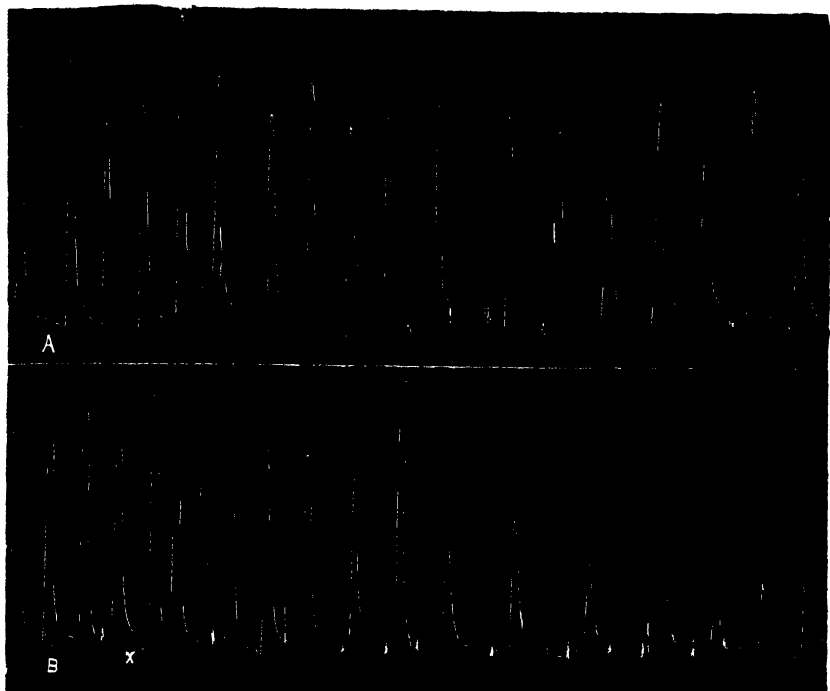
FIG. 32.—Normal digestive peristalsis of frog's stomach. A, three hours after feeding it two small live grass frogs. B, same animal ten hours after feeding, food still in stomach. At x 10 cc. water introduced directly into stomach producing temporary inhibition. Water manometer.

"jumbo" one small frog and then examining from time to time the stomach contents by inserting a pair of forceps through the mouth and esophagus into the stomach, and exposing the digesting animal. I was also interested to find in reviewing the literature, after completing the experiments, that this same method was used by John R. Young (*240*) of Maryland, in 1803, in determining the rate of gastric digestion in the frog as a part of a medical dissertation submitted to the University of Pennsylvania (published in 1805). However, after some experience, I could determine its

condition by palpating over the region of the stomach, and I found by both of these methods that it required from forty-eight to sixty-eight hours for the stomach completely to empty itself. With larger feedings of two, three and four small frogs, the stomach would evidently require a longer period to empty itself. Young did not determine the total time necessary for the stomach completely to empty itself; he simply studied the rate of digestion. In regard to the introduction of water, alkali or acid, it was found that they produced similar inhibitory effects in both the hungry and the filled stomach of the frog (Fig. 32 B), whereas in the case of the higher animals, these same substances inhibit the hunger contractions but have no effect upon the gastric peristalsis with but one exception—the guinea-pig, in which these substances have no effect whatever on either the hunger or the peristaltic movements. This is a little out of harmony with the results obtained from other animals, and one would naturally expect from a comparative standpoint that this animal, judging by the position it occupies in the animal scale, should possess a reflex inhibitory mechanism from the gastric mucosa. King and Connet (*111*) state that they had difficulty in introducing substances directly into the stomach but in a few instances succeeded in introducing about 1 cc. of the various substances. Had they introduced more of these substances would they not have brought out the reflex inhibitory mechanism of this animal? From the above results it would appear that in the frog, at least, we have a much simplified gastric mechanism which, through the processes of evolution, has in the higher animals differentiated into the gastric digestive peristalses and the gastric hunger contractions, the latter of which perhaps may be described as intensified gastric digestive peristalses. Thus, the automatism of the gastric mechanism of the various classes of vertebrates apparently stands in correlation with the degree of development and influence of the central nervous system.

THE INFLUENCE OF TEMPERATURE ON THE GASTRIC ACTIVITY

The influence of temperature on the gastric hunger activity, seasonal variations, and hibernation, in the frog, must be considered under two heads: First, the accelerating action of increased temperature on the chemical processes involved; and second, the inhibitive or retarding action of very high or very low temperatures. Biologic phenomena are undoubtedly largely the result of chemical reactions going on within the living substance, and consequently we would expect that the well-known rule of van't Hoff and Arrhenius concerning the velocity of chemical reactions in relation to temperature, should apply: that is, for each increase of

$10°$ C. in temperature the velocity of a reaction is doubled or trebled. Thus, the above rule, within certain limits, has been verified by Riddle (196) on the process of digestion in cold-blooded vertebrates; by Rogers (198) and Galeotti and Piccinini (81) on the rate of the heart beat for vertebrates and invertebrates; by De Bonis and Midulla (65) for the movements of the frog's stomach by the stomach ring method; and for many other physiological activities.

Tables III and IV show the results obtained from the experiments with the number of contractions executed in the unit of time. The temperature coefficients were obtained as quotients from the formula used by Riddle (196). See p. 104.

<center>TABLE III</center>

<center>Raising the Temperature</center>

Number of contractions per 12 minute intervals— room temperature	Number of contractions per 12 minute intervals after increase of temperature	Temperature coefficient
$23.5°$ C. = rate of 5	$32.5°$ C. = rate of 9	2.00
$25°$ C. = rate of 6	$32.75°$ C. = rate of 10	2.15
$24.5°$ C. = rate of 6	$32.25°$ C. = rate of 10	2.15

<center>TABLE IV</center>

<center>Lowering the Temperature</center>

Number of contractions per 12 minute intervals— room temperature	Number of contractions per 12 minute intervals after decrease of temperature	Temperature coefficient
$20°$ C. = rate of 7	$14°$ C. = rate of 5	2.33
$19°$ C. = rate of 4	$14°$ C. = rate of 3	2.66
$21°$ C. = rate of 6.5	$14°$ C. = rate of 4	2.32

An examination of the data in the foregoing tables shows that the gastric hunger contractions of the frog, within certain not very wide ranges of temperature, follow the rule of van't Hoff and Arrhenius, and furthermore, that the relation between the contractions and the temperature is maintained either when the animal passes from a lower to a higher temperature, or vice versa. Hence, it may be concluded that the gastric hunger contractions of the neuro-muscular apparatus is essentially dependent on chemical processes which are evolved within the stomach muscle itself. In table IV, where the temperature was diminished, there appears to be an increase in the value of the coefficient as zero is approached, which

is entirely in harmony with the observations of Riddle (*196*), and Rogers (*198*). The observations in tables III and IV were made during the month of August, 1915, and three separate animals were used for the results in each table. The findings herewith set forth were verified by control experiments.

I have also been able to carry through a sufficient number of experiments to determine the exact points at which high and low temperatures absolutely inhibit the gastric hunger contractions. The temperatures at which the hunger contractions are completely inhibited are practically constant, for both high and low temperatures, and do not vary more than 0.5° C. in either direction in all the experiments. The average temperatures at which these contractions are completely inhibited is 35° C. for the high temperature and 13° C. for the low temperature. Lowering the temperature 0.5° or at the most 1° in the first case, or raising the temperature 0.5° or at the most 1° in the latter case, starts the gastric hunger contractions again. These experiments were also performed during the month of August, 1915. The intensity of the contractions have a maximum between 15° C. and 32° C. and a minimum at lower or higher temperatures; that is, up to that limit where gastric standstill is produced. Raising the temperature also increases the strength of the contractions as well as the rate, but this effect disappears sooner than the effect of increased rate.

It is a well-known fact that amphibians may be cooled down to –1° C. (*29*), and that their limbs may be frozen in ice (*80*), and that they may survive if the heart is not frozen. But just how does this freezing temperature affect the gastric mechanism? Two of the animals were subjected to temperatures of 7° C. by means of the freezing mixture already described. The hunger contractions were, in a short time, completely inhibited, and the limbs of the animals froze and became stiff and hard and when removed later from the cooling chamber and placed on the table they rattled like stones, although their bodies were not completely frozen. Both the animals appeared lifeless except for a very slow heart beat and infrequent respirations, and their eyes were closed as if they were asleep. One hour later at room temperature these same animals broke the stillness of a mid-summer's night by croaking and began to show feeble gastric contractions which increased in intensity during the next twelve hours but never reached the normal. These observations indicate that the gastric mechanism is capable of movement at all seasons of the year and even in hibernation when given the suitable temperature. If the temperature change is gradual, as at the rate of 10° per three hours, the animal is not disturbed but passes into a drowsy or sleepy state.

X-RAY STUDIES ON THE GASTRIC MOTILITY

The general characteristics of the stomach movements in the frog have been discussed. We have now to consider the genesis of these movements. Two methods of investigation were used, namely, the X-ray and the excised stomach. The X-ray method consisted of introducing into the stomach a double walled balloon, the walls of which were separated by a thin

FIG. 33 —X-ray photograph of the bismuth balloon in the frog's stomach when the graphic record shows the stomach to be quiescent.

layer of bismuth subnitrate mixed with vaseline to form a thin paste (204). The balloon was then connected with the usual recording apparatus and the fluctuations of the float in the manometer served as an indicator for studying the different phases of the gastric movements with the X-ray. From the X-ray studies made on the frog's stomach by means of this bismuth coated balloon, the gastric hunger contractions were found to be peristaltic, the peristaltic waves originating within about 1 cm. of the cardia and then advancing rhythmically over the entire stomach toward the pyloric end, and increasing in strength as they proceeded. These observations on the peristaltic activity of the stomach are in agreement with the X-ray findings reported by Bowditch (22) in the dog, cat,

rabbit, guinea-pig and rat, and by Roux and Balthazard (*206, 207*) in man, dog and frog.   For the X-ray observations the frogs were placed in the box already described for the cooling experiments and this was then placed over the tube generating the rays, which was properly protected. Thus, by looking through a fluoroscope, the gastric hunger peristalsis could be watched with the X-rays. A series of X-ray photographs was taken of the balloon in the frog's stomach during the periods of rest and at varying intervals during the period of gastric hunger contraction, the special radiographic plate being inclosed in the red envelope and care-

FIG. 34 —X ray photograph of the bismuth balloon in the frog's stomach at the height of a moderate hunger contraction

fully placed on the frog's back (Figs. 33, 34 and 35). In every case the contraction and the relaxation of the stomach corresponded precisely with the graphic record (Fig. 30).

The studies on the excised stomach showed the same general phenomena as presented by the X-ray observations above. The stomach was removed with the esophagus and the intestine. The balloon was introduced into the stomach and the esophagus ligatured to the tube upon which the balloon was attached. This was connected with the recording apparatus and the stomach was placed in Ringer's solution at 30.5°C., which had been found by the temperature experiments to be a most favorable temperature

for gastric activity, and into this solution was led a slow current of oxygen. The rate of the contractions increased but the amplitude was lessened as compared to the normal gastric movements (Fig. 36). In other words, the stomach had lost its regulatory apparatus, the extrinsic nerves which govern normally the rate, size and strength of the gastric movements. These contractions from the excised stomach showed an average duration of about thirty seconds with practically no intervals of rest between the in-

Fig 35 —X ray photograph of the bismuth balloon in the frog's stomach at the height of a very strong hunger contraction

dividual contractions. Increasing the pressure in the balloon does not necessarily raise the tonus; the stomach simply dilates until the limit of expansion is reached. This confirms the results on the living animal, obtained from the stomach *in situ*, which have already been described. Dropping the temperature even a few degrees reduces the size of the contractions. The curves show a distinct tonus rhythm with practically no changes in the general gastric tonus. The stomach also shows contractions with an uninflated balloon in it, as well as when it is completely empty and collapsed, but the peristaltic contractions are feeble, due to the fact that the organ is collapsed and not in a suitable condition to ex-

hibit the full strength of the contractions. The cardia, however, is the first part of the stomach to exhibit motor activity and the last part to show it. The peristaltic waves appear to originate at the upper end of the gastric tube at a tonus ring near the cardia, which forms a more or less marked depression known by X-ray workers as the "incisura cardiaca" (*84*), and from this point the waves sweep over the stomach toward the pyloric end as in the case described under the X-ray observations. The peristalsis observed in the frog's stomach does not always bear the character of rapidly running waves, but in certain cases may have a tonic character similar to the tonic contractions forming deep rings, thus giving the stomach the form of an hour-glass. But when these contractions are carefully analyzed, they are found to be peristaltic throughout. These observations are in confirmation with those of Pletneff (*189*) on the isolated stomachs of cats and pups, with the exception that the peristaltic waves begin at the middle of the stomach rather than near the cardia, but they are contrary to the findings of Dixon (*68*) and Morishima and Fujitani (*150*) who claim that the contractions of the stomach wall follow no strict conformable order and that the contraction rings generally show little tendency to spread. Therefore, according to these authors, the movements of the frog's stomach are not peristaltic. However, X-ray observations by various investigators have conclusively shown the movements of the stomach to be peristaltic.

THE EFFECT OF DECEREBRATION ON THE GASTRIC ACTIVITY

We know, particularly through the researches of Carlson (*42*) on the higher animals (man and dog), that the gastric hunger contractions are inhibited by psychic stimuli, and that at least in the dog they continue even after the stomach has been isolated from the central nervous system by section of the vagi and splanchnic nerves. Under these conditions stimulation of the gastric mucosa also produces the characteristic reflex inhibition but to a lesser degree than normally. It is also known that the stomach passes into a permanently hypotonic condition after double vagotomy (*44*). King and Connet (*111*), working with decerebrate guinea-pigs, have reported that the rate of the gastric contractions is increased, although similar in character to those from the normal animal, and also that the stomach becomes hypertonic. However, in the frog the gastric hunger contractions are not affected by the removal of the cerebral hemispheres, the graphic record of the normal and the decerebrate animal remaining practically the same (Fig. 37 A and B). Since the removal of

this organ produces no apparent effect on gastric motility, it may be inferred that what controlling influence the brain exercises over the stomach of this animal comes from centers in the mid-brain and medulla and not from those of the cerebrum. This idea is in agreement with the more recent work of Miller (*148*) on dogs, who by means of unipolar stimulation in the floor of the fourth ventricle has localized in the dorsal vagus nucleus (ala cinerea) centers for cardiac inhibition and for movements of the stomach and small intestine. In the higher animals cerebral processes of pleasantness, such as the appearance of a friend, and unpleasantness such as fear, anger, fright, etc., reflexly inhibit the rate and tonus of the gastric movements, whereas in the case of the frog similar reflex inhibitory action on gastric motility is only exhibited to a very slight degree. This demonstrates again the simplified gastric

FIG. 36.— Tracing from the excised stomach of the frog, showing a marked tonus rhythm. Water manometer.

mechanism of the frog and that the cerebral processes exert no appreciable influence on the gastro-neuro-muscular apparatus. Eight animals were decerebrated, all of which confirmed the above results, even one in which the semi-circular canals were injured, and all exhibited the characteristic exaggeration of the reflexes. In figure 37 B the contractions do not appear quite as high as in the normal animal. However, in other cases they have been found even to exceed the normal.

To summarize: the simpler gastric mechanism of the frog does not show the distinction between the digestive peristalses and the hunger contractions, present in the higher animals. There is no increase in gastric tonus and the hunger contractions are practically continuous. The hunger contractions are inhibited or weakened by the introduction into the stomach of small quantities of water, weak alkali, and acid, but the inhibitory effects are not produced as quickly as in the higher animals. When these substances are introduced into the mouth of the frog, the inhibitory ef-

fects are very slight, but when introduced into the filled stomach of the frog they inhibit the digestive peristalsis in the same degree as they inhibit the hunger contractions of the empty stomach. In the higher animals normal digestive peristalsis is not inhibited by these substances in the same amounts. During prolonged fasting the hunger movements are greatly augmented and the contractions show a marked increase in the amplitude, directly proportional to the length of the fast, but no increase in gastric tonus. In the higher animals like the dog there is a marked increase in the gastric tonus in prolonged fasting, and this increase is inversely proportional to the decrease in the amplitudes of the hunger contractions.
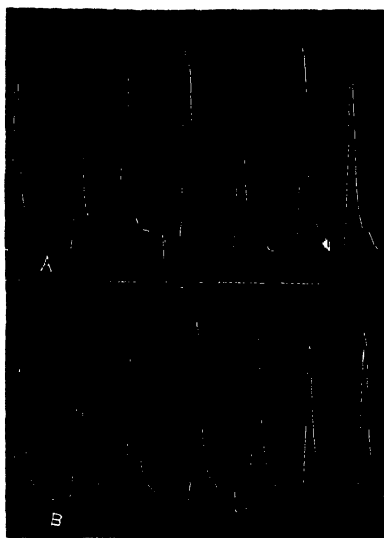
FIG. 37.—Records from the stomach of the normal and decerebrate frog. A, contractions from the normal stomach after three and one-half days' fast, stomach empty. B, contractions from the same animal's stomach, twenty-one hours after decerebration. Note that the contractions in A and B are practically identical in rate and form. Water manometer.

The hunger contractions of the frog's stomach are completely inhibited at 13° C. for low temperature and at 35° C. for high temperature. Raising the first temperature or lowering the second 0.5°, or at the most 1°, starts the hunger contractions again. Furthermore, the gastric hunger activity is proportional to the climatic changes in temperature within certain limits, as is indicated by van't Hoff's rule. The movements are peristaltic and the waves start near the cardia at the "incisura cardiaca." The stomach of the decerebrate animal behaves in the same manner as that of the normal frog.

Much has been written concerning the excitatory and inhibitory influences of the vagi and splanchnic nerves upon the gastric motility and

a rather thorough review of the literature covering this phase of the question has already been discussed. In addition, the distribution and function of the nerves innervating the visceral and vascular systems in crocodiles and alligators was worked out by Gaskell (*82*). He found that stimulation of the peripheral end of either vagus above or below the ganglion trunci vagi invariably led to a contraction of the stomach musculature. After section of the cervical vagus above the ganglion, with subsequent degeneration of its fibers, stimulation above the ganglion almost invariably produced no effect whatever on the esophagus and stomach, while stimulation below the ganglion almost invariably caused marked peristaltic contraction. Gaskell came to the conclusion that the fibers which innervate the thoracic portion of the esophagus and the stomach, and in all probability the intestines, degenerate only in the portion which is above the ganglion, and not in the portion below the ganglion; and that the nerves for the upper part of the esophagus and the inhibitory fibers of the heart have no connection with the nerve cells of the ganglion trunci vagi, while the motor nerves for the rest of the esophagus and the upper portion of the remainder of the alimentary canal are in connection with the cells of that ganglion—a connection by which the motor fibers proceeding peripherally from the ganglion, but not the motor fibers which pass to the ganglion, are prevented from degeneration.

Furthermore, the recent observations, by the balloon method, of Crohn and Wilensky (*61*) on gastric behavior, have shown that in atony of the stomach the hunger contractions disappear and in advanced cases the tonal waves also, while in purely secretory or other functional disturbances both kinds of waves persist.

In this series of experiments, normal contractions of the empty stomach, extending over a period of several days after stomostomy, were obtained from each animal, and then each of these animals was operated on a second time. In this second operation, either both vagi or both splanchnic nerves, or both the vagi and the splanchnic nerves together, were sectioned, followed after recovery in each case by a series of tracings from the empty stomach. The animals were anesthetized with ether. Aseptic precautions, as far as possible, were at first followed, but later this was found to be unnecessary as no infection developed in any of the animals when such procedure was not followed. The vagi were sectioned in the region of the neck. Two oblique incisions were made through the skin on either side of the median line, ventral, about 1 cm. distant, and close to the anterior tips of the shoulders as represented by a line drawn from this point laterally, 1 cm. to 1¼ cm. in length, to a point slightly posterior,

and just internal to, the articulation of the superior and inferior maxillary bones on either side. These two incisions exposed the cervical fascia on either side at its attachment along the anterior scapulo-clavicular borders. Here there are few blood vessels and if the fascia is carefully separated no hemorrhage results. As soon as this region is passed the fascial separation becomes very easy until the thin sheet of prevertebral fascia is reached, which is about on a line of the transverse processes passing obliquely downward and inward from the base of the skull and extending into the thorax. This latter sheet of fascial membrane is now pierced, which exposes the levator anguli scapulæ muscle, over the anterior border of which courses the vagus nerve and the internal jugular (Vena jugularis) and musculo-cutaneous (Vena musculo-cutanea) veins. The incision is held open by the spring of a small pair of forceps (preferably curved points) and then by means of a small pair of mouse-toothed forceps the nerve is carefully separated from the adjoining veins to which it is bound by connective tissue. This is best accomplished by freeing the nerve either between the two veins mentioned or just lateral to the internal jugular vein at the anterior border of the levator anguli scapulæ where it crosses, and sectioning the nerve just below the origin of the recurrent laryngeal branch. Section of the nerves at this point destroys not only the gastric branches to the stomach but also the pulmonary and cardiac branches destined for the lungs and heart. Attempts were made at first to section only the gastric branches, but as these branches were so small and so deeply embedded in the tissues it was found to be practically impossible if the animals were to recover. In fact, the technique as used required several months' experience before it became perfected and only then did it become an efficient procedure which, if properly handled, may be called a bloodless method. Both vagi were always sectioned at one operation and the skin incisions were closed with five sutures.

The splanchnic nerves were sectioned in the region of the cœliac plexus, after laparotomy. An incision was made through the skin, the rectus abdominis muscle, and the aponeuroses of the external and internal oblique muscles, 2.5 to 3 cm. in length, extending from the lower extremity of the sternum (xiphisternum) caudalward and about 0.5 cm. to the left of the linea alba, in order to avoid the anterior abdominal vein (Vena abdominalis) which courses forwards along the mid-line of the ventral body wall until opposite the liver. The stomach is withdrawn through this opening and a large pair of nerves, one on either side, is found coursing along with the right and left systemic arches. These are the third spinal nerves carrying fibers to the stomach, but according to Steinach

and Wiener (*216*), Dixon (*68*) and others, the stomach also receives fibers from the fourth and fifth spinal nerves and Waters (*237*), in addition includes the sixth.

Fibers from these nerves arising from both sides of the body unite to form the cœliac plexus situated on the cœliaco-mesenteric artery (Ateria intestinalis communis) a few millimeters from its origin from the left systemic arch. From this plexus arise the nerves destined for the stomach, pancreas and duodenum. The branches for the stomach are imbedded in the mesenteric membrane and follow closely the course of the arterial supply of this organ. They may be best seen by raising the stomach and allowing the light to illuminate the mesentery when they may be picked up with mouse-toothed forceps. If they are cut close to the plexus there are usually not more than two branches. Experience has shown that it is advisable to introduce into the stomach 5 or 6 cc. of water previous to the operation as it tends to fill and round out the stomach, thus making it easier to locate the plexus and the nerves. The technique for this operation. like that for double vagotomy in the frog, is very delicate, but with sufficient patience and experience it may be developed to such a point as to be conducted without hemorrhage, and like the former may be considered a bloodless method. The splanchnicotomized stomach is pushed back into place, the muscular incision is closed with nine to ten sutures and the skin incision with the same number. The animals, after double vagotomy or splanchnicotomy, are usually sufficiently recovered on the third day following the operation to be used for experimental tests with fairly marked gastric activity, while after the double operation they are usually not ready for use until the fourth day following the operation. In the decerebration experiments the balloon was not removed from the stomach, and the gastric contractions started again after a short period of inhibition.

A complete knowledge of the mechanism of the gastric movements is still uncertain. The gastric activity is regulated not only by the vagi and the splanchnic nerves of the sympathetic system, but also by the automatically acting plexi of Auerbach and Meissner. The most direct and desirable method of attack on this problem is the section of the extrinsic nerves to the stomach, although this operation abolishes not only all direct influences from the brain, of a motor or inhibitory type, but also the central reflexes (motor or inhibitory) that may be called into action through the sensory nerves in the stomach.

The influence of these nerves on the activity of the stomach has been studied by a number of investigators, prominent among whom have been Cannon (*30, 33*) and Carlson (*44*). Cannon's observations on the gas-

tric movements of digestion in cats have shown that section of the vagi leads to a temporary loss of tonus and a slowing and weakening of the peristalsis, which in respect to rate is practically restored in a few days. He infers as does Kelling (*109*) that their function is solely to make the gastric muscles exert a tension (tonic state) and the result of this condition is peristalsis. Furthermore, section of the splanchnic nerves does not affect the movements of digestion, while the combined vagi and splanchnic section leaves the digestive movements of the stomach practically normal, even shortly after the operation.

Carlson (*44*), on the other hand, has shown that section of the vagi in dogs leaves the empty stomach on the whole permanently hypotonic, at least for a period up to three months after the operation. Section of the splanchnic nerves increases the gastric tonus and augments the gastric hunger contractions, while the section of both the vagi and the splanchnics leads to a permanent hypotonus of the stomach, except under conditions of prolonged fasting. These discrepancies between the results of the two investigators are probably accounted for by the fact that the tonus of the vagus plays a greater rôle in the movements of the empty, than in the movements of the filled stomach; or else the nerves vary in different species of animals.

THE EFFECT OF COMPLETE SECTION OF THE SPLANCHNIC NERVES

Complete section of the splanchnic nerves on both sides in the region of the cœliac plexus was made on twelve frogs and after recovery from the operation records of the movements of the empty stomach were continued from two to three weeks and compared with those from the normal stomach of the same animal.

When a comparative study of the records of these animals is made as a whole, it is evident that the complete section of the splanchnic nerves with the vagi intact, markedly increases the gastric tonus and augments the movements of the empty stomach in frogs (Fig. 38 A and B). The recorded contractions are small, rapid and irregular in form, and represent virtually an incomplete or hunger tetanus of the stomach. In other words, the stomach becomes on the whole strongly hypertonic and more active through the destruction of the inhibitory fibers via splanchnic nerves to the stomach, which permits the motor fibers of the vagi to exert their full influence on the gastric motor mechanism, thus leading to a degree of gastric tonus much above the normal. This particular state of excessive tonus is evidenced not only by the balloon in the stomach cavity but more especially by the marked contraction of the esophagus and stom-

ach as is instanced many times by the extreme difficulty of introducing the balloon through the esophagus into the stomach. This hypertonic condition of the frog's stomach, which always appears after complete section of the splanchnic nerves, is evidently more marked than Carlson (44) found it to be after splanchnic section in dogs. Furthermore, this condition, as it exists in frogs after this type of nerve section, apparently corresponds to certain clinical conditions as reported by Eppinger and Hess (76) under the term "vagotonia." According to these observers, the antagonistic influences between the gastric branches of the vagi and the splanch-
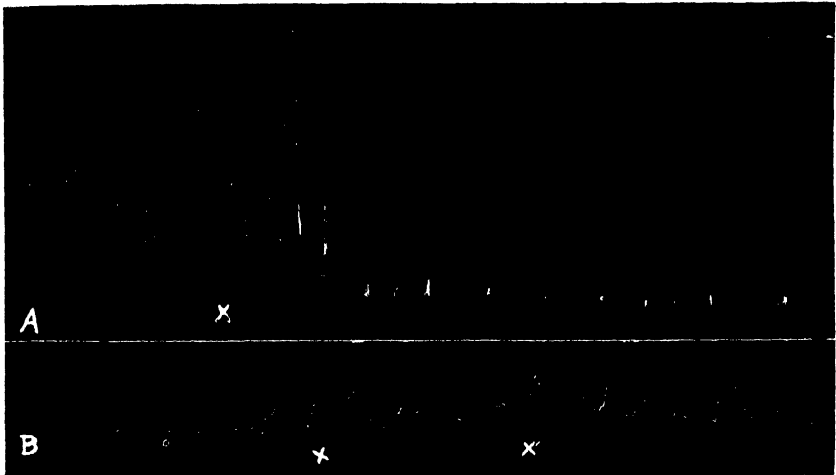
Fig. 38.—Records from the empty stomach of the frog. A, normal frog after six days' fast; B, the same animal ten days after section of both splanchnic nerves and twenty days' fast. At x, introduction of 5 cc. of 0.5 per cent. solution of hydrochloric acid directly into the stomach. Showing incomplete tetanus and only slight inhibition of the hunger contractions by acid in the stomach after section of the splanchnic nerves. x'= termination of the acid injection.

nic nerves play a very important rôle in not only moderating the physiological impulses which might reach a very marked intensity, but in addition they prevent acute transitions from rest to excitation or vice versa. This means that if it were not for the above, small stimuli might under certain conditions cause large reactions, either physiological or pathological. Now, if we assume that somewhere in the central nervous system there exists a common center which controls the antagonistic actions of these two systems, as suggested by these investigators, and that the irritability of this center increases and decreases from time to time, it is easy to understand how very weak and even transitory stimuli might act upon such a

center—when in a state of increased irritability—to produce the gastric hypertonus through the fibers of the vagi. This, however, is not proven, but we do know that in the condition of vagotonia there is a functional increase of tone via vagi to the stomach, and this increase of function doubtless permits the stimuli to act more readily than if the reversed condition existed. Furthermore, the observations of Crohn and Wilensky (*61*) have shown that the hunger contractions in well marked cases of vagotonia exhibit an extreme degree of variability, the contractions following one another in rapid succession and without pause for comparatively long periods of time. The clinical findings of these observers are apparently in accord with the results on frogs, after splanchnic section.

The inhibition of the movements of the empty stomach of the splanchnicotomized animal, when acid is introduced into the stomach cavity, is much less complete than in frogs with all the extrinsic gastric nerves intact (Fig. 38 A and B). In fact, the contractions do not cease at all; and the only effect produced is a very slight decrease in the height of the contractions during the introduction of the acid, followed by a few contractions of a slightly longer duration, and usually a slight increase in the gastric tonus. This diminution of the inhibition, following stimulation of the gastric mucosa by acids after complete section of the splanchnic nerves, is confirmatory of Carlson's findings (*45*) on dogs.

THE EFFECT OF SECTION OF BOTH VAGI NERVES

Section of both vagosympathetic nerves in the neck was made on eleven frogs and after recovery from the operation records of the movements of the empty stomach were continued from two to three weeks and compared with those from the normal stomach of the same animal.

When all the records are compared from these animals, the results are confirmatory in showing that the contractions of the empty stomach are only slightly changed in rate and regularity. The contractions, when viewed as a whole, resemble those from the normal stomach, with the exception that they usually appear to be of a slightly slower rate, and weaker and more irregular (Fig. 39 A and B). However, there is a tendency for the contractions to increase in strength—or rather amplitude—up to the amplitude of the normal contractions, and some of the individual contractions may even exceed the normal. This is evidently produced through a lowered tone in the gastric motor mechanism, whereby the contractions start rather suddenly and without any marked preliminary increase in tonus; and because of this condition the air is more com-

pletely forced out of the balloon, thus resulting in the greater contraction. In the empty stomach of the normal animal, as determined by the balloon method, there are practically no tonus changes, or at least they are so slight in degree as to be almost a negligible factor. In working with these animals, over a period of several years, I have never observed
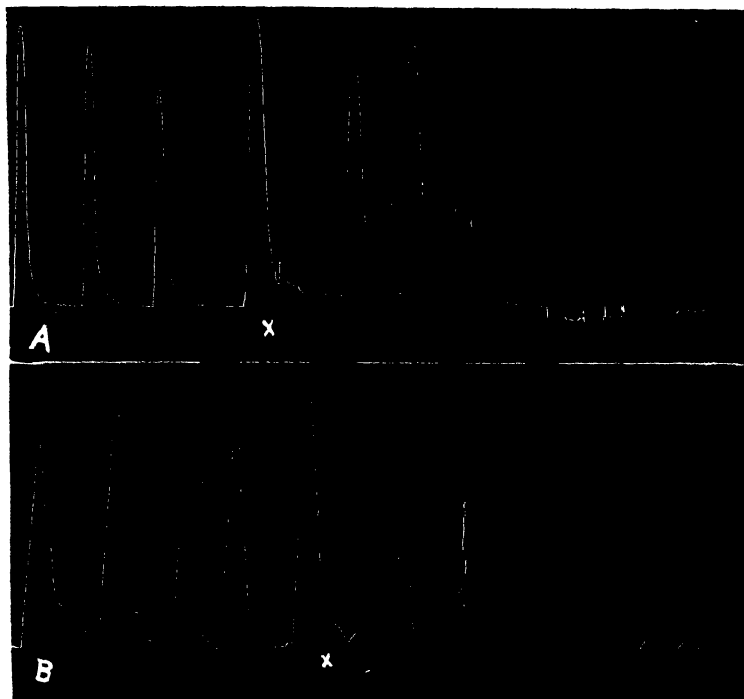
Fig. 39.—Records from the empty stomach of the frog. A. normal frog after three days' fast; B. the same animal nine days after section 'of both vagi and sixteen days' fast. At x introduction of 5 cc. of 0.5 per cent. solution of hydrochloric acid directly into the stomach. Showing slightly more complete inhibition of the hunger contractions by acid in the stomach after section of the vagi nerves.

in the normal animal an increase in gastric tone exceeding a centimeter, as determined by the manometric pressure. When tonus changes are observed they usually do not exceed a quarter of a centimeter (2 to 3 mm.), unless it is in cases of very extreme periods of fasting. But the more common phenomenon in the frog is to have the tonus remain constant hour after hour.

Section of both vagi with the splanchnics intact leads to a sympatheticotonic condition of the stomach. This means that the stomach becomes

on the whole hypotonic through the destruction of the vagal fibers which maintain the gastric tonus. This permits the inhibitory fibers of the splanchnics to exert a greater influence on the gastric motor mechanism, thus leading to a general diminution in the gastric tonus. However, there was a tendency in some of the animals, at least, to show a gradual improvement in the efficiency of the local tonus mechanism as time went on, after the operation, which indicated that the hypotonic condition of the stomach may be only temporary in the frog and not permanent as reported by Carlson (44) in dogs, but corresponds to the observations of Cannon (*30, 33*) in cats for the movements of digestion. This phase of the question will be discussed in another section of this paper. Furthermore, the gastric tonus is much lower on the whole than normal, as determined not only by the balloon in the gastric cavity, but also by the ease with which the balloon may be introduced through the esophagus into the stomach, and inflated.
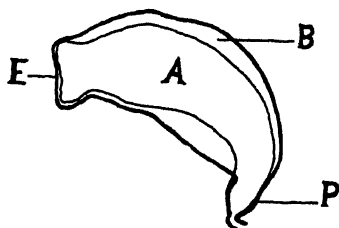
FIG. 40. — Splanchnicotomized stomach superimposed upon the vagotomized stomach from two frogs of equal size, weight and vigor. A, splanchnicotomized stomach. B, vagotomized stomach. E, esophagus. P, pyloric portion of stomach. Note the hypertonic condition of stomach A.

When acids are introduced directly into the empty stomach of the vagotomized animal, gastric inhibition is exhibited similar to that produced in the normal animal except that it appears to be quicker and more marked than in the normal animal (Fig. 39 A and B). This is exactly contradictory to Carlson's results on dogs (*44*); yet he states that this was what he expected to find, namely, an augmentation of the inhibition through the splanchnics after section of the vagi.

THE EFFECT OF COMPLETE SECTION OF THE VAGI AND SPLANCHNIC NERVES

Combined splanchnic and vagi sections were made on ten frogs and after they had recovered from the operation records of the gastric movements were continued for from two to three weeks and compared with those from the normal stomach of the same animal. Both sets of nerves were sectioned at the same operation.

After this complete isolation of the frog's stomach from the central nervous system, the movements of the empty stomach are much the

same as when the vagi alone are severed. The contractions show a tendency to approach or even in some cases to exceed the normal, while at times they may even be identical in rate and character with those of the intact stomach. For the most part, they are of a slightly slower rate and more irregular. The stomach passes into a hypotonic condition similar to that after section of the vagi, and therefore the slight changes in the movements of the empty stomach after isolation from the central nervous system must be due primarily to the persistent hypotonus. These results are, in general, confirmatory of Cannon's (*30, 33*) on cats and of Carlson's (*44*) on dogs.

The inhibition of the movements of the empty stomach by acid stimulation of the gastric mucosa persists after complete isolation of the stomach from the central nervous system but the inhibition, like that found by Carlson (*45*) in dogs, is diminished in intensity and duration. There is a gradual and slow diminution, both in the rate and amplitude of the hunger contractions, but as a rule this does not produce complete inhibition in the frog. The inhibition is therefore primarily a local reflex determined by the local gastric mechanism rather than by the character of the central innervation or the central inhibition. Since the type of gastric activity after complete isolation of the stomach from the central nervous system does exhibit the typical movements of the empty stomach, the primary stimulus to these contractions is not to be sought in the extrinsic nerves. The extrinsic nerves (vagi and splanchnics) must therefore be considered under normal conditions to play the important rôle of modifying or regulating a primary automatic mechanism in the stomach wall.

EXTIRPATION OF STOMACHS AFTER SECTION OF VAGI AND SPLANCHNIC
NERVES

Early in the course of these experiments it was observed that the stomachs of splanchnicotomized and vagotomized animals exhibited rather wide variations in size, depending on whether the vagi or the splanchnic nerves had been previously severed. This phase of the problem was investigated on ten splanchnicotomized and ten vagotomized animals, and the stomachs were removed from three to ten days after the operation, directly after the killing of the animals and while the hearts were still beating. In the selection of these animals care was taken to select frogs of equal size, weight and vigor. The results of these experiments are conclusive in showing that the same general influence which the vagi and splanchnic

nerves exert separately on the gastric apparatus may be shown when the splanchnicotomized stomach is superimposed upon the vagotomized stomach from two frogs of equal size. The latter or larger stomach represents the atonic, and the former or smaller the hypertonic, while the normal stomach takes an intermediate position between the two (Fig. 40). It may be said, therefore, that the reciprocal or contrary innervation of Meltzer, which may be termed antagonistic tonus, may be physiological as long as it serves the purposes of the organ in question in a beneficial manner. It is pathological as soon as the tonus of one or the other is so exaggerated that the common welfare of the organ is in danger. That is exactly what happens in the splanchnicotomized frog's stomach, where the hypertonus of the vagus leads to a state of overexcitability, or to the Eppinger-Hess condition of vagotonia.

PSYCHIC OR REFLEX INHIBITION OF THE GASTRIC HUNGER MOVEMENTS

It was thought early in the course of this investigation, that it might be well to study certain cerebral processes in relation to the reflex effects on gastric activity. Previous work on other animals has demonstrated that anything which interests, annoys, frightens or angers, leads to a temporary inhibition of the gastric hunger contractions, probably via splanchnics. Furthermore, the sight or smell of food, in the dog at least, leads to this same temporary inhibition if it is not too often repeated. In order to test further the very important reflex control of the gastric hunger mechanism, as well as of the nervous foci in the medulla, mid-brain and cerebrum concerned in the conduction of sensory and motor hunger impulses, the effects of sound and light stimuli were made use of in the following experiments. The observations were made on six frogs which were later decerebrated and the observations repeated. In the case of the sound stimuli, whistles of different pitches were sounded for periods of from ten to twenty seconds, but these caused only very slight gastric inhibition which was of short duration; after two or three repetitions it invariably became ineffective, thus defeating the object of the experiment. Even the filing of a glass rod on the table containing the animal was fully as ineffective in producing inhibition, although a second factor must have been introduced, that of vibration. All of these stimuli were of minimal or very moderate intensity and evidently not of sufficient strength to produce an effective and constant reflex—or else the central nervous mechanism for this reflex is at a low degree of development.

The light stimulus, on the other hand, proved to be more effective. The

room was darkened by drawing the window shades and while the normal
hunger contractions were being recorded the animal was carefully un-
covered and the lower portion of the window shade directly opposite drawn
back and forth quietly and at a moderate rate, thus casting light and
dark shadows upon the animal. This invariably produced temporary
inhibition of the movements of the empty stomach and there seemed to be
no diminution in the degree of the inhibition after repeated trials. After
removal of the cerebral hemispheres there was total absence of the reflex
inhibition and the contractions went on uninterrupted. It would appear
that the central nervous mechanism for this reflex was more highly devel-
oped than that for sound. In other words, from the animal's standpoint
it may be considered an important defensive reflex to warn it of its avian
enemies as they soar through the air; thus anxiety and fear lead to the
characteristic temporary inhibition of the gastric hunger movements.

When the light and darkness shadow test was applied to an animal
after complete section of the vagi with the splanchnics intact, it in-
variably led to a temporary inhibition of the gastric hunger movements
via splanchnic nerves (Fig. 41 A). If the same test was applied to an
animal after complete section of the splanchnic nerves with the vagi in-
tact, it unfailingly led to only a very slight inhibition of the gastric
hunger movements, as represented by a slight and transitory weakening
of the contractions (Fig. 41 B). This slight degree of inhibition usually
in evidence after section of the splanchnic nerves is probably the result
of the action of the few inhibitory fibers in the intact vagi, or to some
central inhibition of vagus tonus. In the case of the stomach completely
isolated from the central nervous system (vagi and splanchnic nerves
cut) there is total absence of any psychic or reflex inhibition, since the
efferent nerve pathways to the stomach have been broken by the section-
ing of all the extrinsic nerves (Fig. 41 C).

To summarize: Complete isolation of the frog's stomach from the cen-
tral nervous system leads to hypotonus of the stomach with about the
normal type of gastric hunger contractions. This is in confirmation of
the work of Carlson on dogs. The automaticity of the gastric mechanism
is independent of the extrinsic nerves, but these nerves play an important
rôle in modifying or regulating the automatic mechanism in the stomach
wall. Partial isolation of the stomach from the central nervous system
interrupts the normal antagonistic balance between the vagi and splanch-
nic systems, which may lead to pathological reactions such as vagotonia
after complete section of the splanchnic nerves. The stomach in this
condition becomes strongly hypertonic, while after complete section of

the vagi with the splanchnics intact the stomach passes into a hypotonic
condition.

The acid inhibition of the movements of the empty stomach by stimu-
lation of the gastric mucosa, persists after complete isolation of the stom-
ach from the central nervous system, but the inhibition is diminished
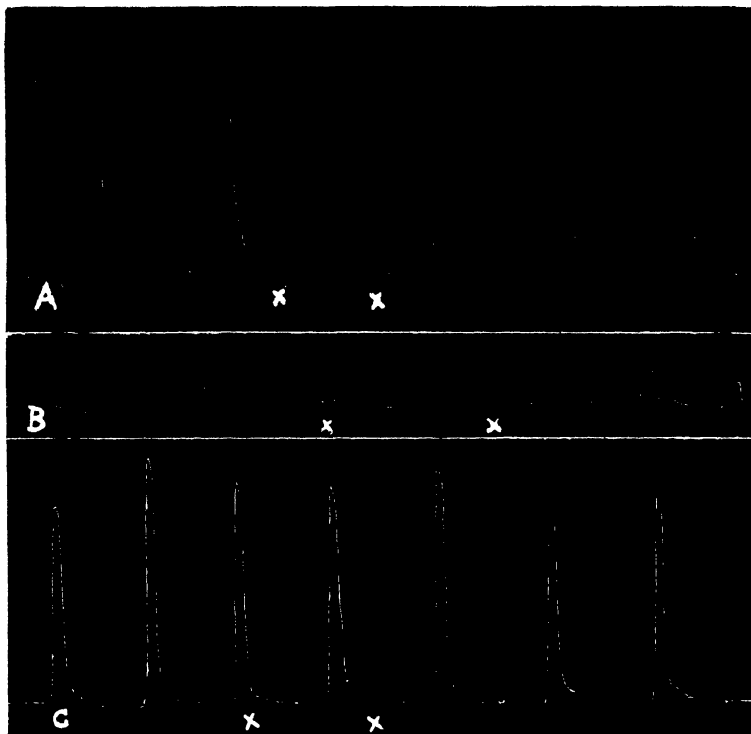
FIG. 41.—Records from the empty stomach of frogs. A, frog nine days after section
of both vagi with splanchnics intact; B, frog eight days after section of both splanchnic
nerves with vagi intact; C, frog nine days after section of the vagi and splanchnic
nerves. x to x, light and darkness shadow test showing temporary inhibition in A,
very slight inhibition in B, and total absence of psychic or reflex inhibition in C, in
the case of the stomach isolated from the central nervous system.

in intensity and duration. When the splanchnics alone are sectioned the
inhibition is even less marked, but after section of the vagi with the
splanchnics intact there is, on the whole, a slight augmentation in the
inhibition, via these nerves. This latter statement is contradictory to
the findings of Carlson (44) on dogs, while the other facts above are in
accord. The light and darkness shadow test invariably produces psychic

or reflex inhibition of the gastric hunger movements in the normal animal. After decerebration, or after complete isolation of the stomach from the central nervous system, there is total absence of the light reflex on the gastric mechanism. When the vagi alone are sectioned, temporary inhibition is the result, while after section of the splanchnics with the vagi intact there is only very slight inhibition produced.

Sherrington (*211*) in 1915 called attention to the reflex postural activity of muscle and nerve as being the main outcome of the functioning of the proprioceptive part of the nervous system for at least the skeletal muscle. He pointed out that the muscle fiber possessed the property of exhibiting different lengths, while exhibiting one and the same degree of tension, and that it was not to be regarded as an elastic band. Furthermore, he believed that unstriated muscle, like skeletal muscle, possesses the same properties, as is shown by the ease with which the hollow visceral organs, like the bladder and stomach, adapt their size to the volume of their contents, and with very little alteration in their intravesical pressure. Under these conditions, therefore, visceral tonus is, postural configuration. In confirmation of this, Hurst (*96*) found that the relaxation of the rectum was analogous to what Sherrington described as the "lengthening reaction" of the "postural tone" in the skeletal muscles and in the bladder, and which he at an earlier date had described in connection with the stomach and intestine, although he had not actually used the expression "visceral tone." In case of the skeletal muscle the reflex postural action depends normally upon the afferent nerve of the posturing muscle itself, while in the unstriated muscle it is far less dependent on the central nervous system for its adjustment and maintenance.

More recently Grey (*89*) has shown by slowly filling the empty viscus with warm physiological saline solution, and recording the fluctuations in the intragastric pressure, that the normal stomach in rabbits and cats is capable of adapting its size to the volume of its contents, with very small changes in the intragastric pressure. According to this investigator, the mechanism involved in the postural configuration of the stomach is situated in the wall of the viscus itself and concerns solely its musculature, together with its intrinsic nervous mechanism, while the extrinsic nerves exhibit no direct influence, but serve rather to regulate the tension of the stomach wall.

The experiments of the author (*171*) here summarized were undertaken with the view of securing further data on the gastric tonus (postural activity—Sherrington, Hurst, Grey) of the neuro-muscular apparatus as applied to the empty stomach. While the term "postural activity" is

very applicable to the skeletal musculature, it seems to me that it is not well suited for the unstriated musculature which makes up the larger portion of the walls of the hollow visceral organs; therefore, the older and simpler terminology of gastric tonus will be used in this discussion. The results tend to show that the extrinsic nerves exert a partial influence on the tonal activity of the stomach viscus, as well as serving to modify and regulate the gastric activity, at least in the frog. This animal is particularly adapted for such a study, for it has been demonstrated elsewhere that the gastric hunger contractions show no periodicity and no appreciable change in gastric tonus, both features of which are present in the higher animals. In contradistinction to the higher animals, the contractions are practically continuous, with scarcely any distinction between the digestive peristalsis and the hunger movements.

Among the first to make observations upon the internal pressure of the hollow visceral organs were Mosso and Pellacani (*151*) who investigated the bladder in man and in the dog. These authors found that the bladder is capable of adjusting its cavity-volume to different quantities of content, which it enfolds with about the same light tension of grasp whether the viscus is nearly empty or well filled. Somewhat similar observations have been made upon the fundic portion of the stomach. Kelling (*109*) found that within certain limits the intragastric pressure remained unaffected by the quantity of fluid within the viscus and that the intra-abdominal pressure altered very little in the dog before and after the taking of a copious meal, although the intake of the volume of food might amount to 50 per cent. of the total contents of the abdomen in the fasting condition. He infers from these latter observations that the additional volume of contents must be accommodated by a reflex adjustment of the postural contraction of the abdominal muscles. Pike and Coombs (*187*), in confirmation of the above, have reported that the introduction of fluid into the stomach, or into the peritoneal cavity of cats, causes lengthening of the rectus abdominis muscle while the flow of fluid out of the stomach causes a shortening of the same muscle. These changes in the length of the muscle are small and do not occur if the posterior roots of the spinal nerves supplying the muscle have been cut, or if the spinal cord has been transected at the level of the lower cervical roots. The section of both vagi has no marked effect on the response of the muscle. The authors regard the change in the length of the muscle, corresponding to the increase or decrease in volume of the contents of the abdominal cavity, as a reflex process dependent upon afferent impulses; this falls into line with other known instances of postural ac-

tivity of muscle and nerve. The observations of Sick and Tedesko (*213*), and of others, have shown that the gradual filling of a cat's stomach is not accompanied by a rise in intragastric pressure, and that the excised stomach, kept alive in a bath of warm oxygenated Ringer's solution, also exhibits the same phenomenon to an unmistakable extent.

Cannon and Lieb (*36*) have also brought forth evidence that each passing of the cardia by swallowed food is accompanied by a rapid small dilatation of the fundus, and that this dilatation is a reflex operated through the vagus. Rogers (*202*) has reported that central stimulation of one vagus nerve with the opposite nerve intact in the decerebrate dog, and after complete splanchnic section, leads to reflex spasmodic contractions of the entire stomach and increased gastric tone. It would therefore appear that the adaptability of the normal stomach is at all times a form of receptive expression brought about by changes in the intragastric pressure, as the volume of its contents slowly increases or decreases.

The same general method was used in the following experiments, with the exception that the gastric balloon was inflated with a known quantity of air by means of a graduated glass syringe sufficient to maintain a constant pressure of 2 cm. in the water manometer, and the number of cubic centimeters of air necessary in the different experiments to produce this constant pressure was recorded. Normal contractions of the empty stomach were obtained from each animal, extending over a period of several days, and then these animals were either vagotomized, splanchnicotomized or vago-splanchnicotomized (section of both sets of nerves), and the respective observations were repeated over a period of from two to three weeks and compared with the normal. The recorded tracings were taken on a slowly moving drum making a revolution in fifty to sixty minutes.

THE CHANGES IN VOLUME CAPACITY OF THE STOMACH AS INFLUENCED BY PARTIAL AND COMPLETE ISOLATION FROM THE CENTRAL NERVOUS SYSTEM

The influence of the vagi and splanchnic nerves on the activity of the empty stomach of the frog has already been discussed. According to these results, double vagotomy leads to a sympatheticotonic condition of the stomach, followed with nearly the normal type of hunger contractions except that they appear to be of a somewhat slower rate and slightly weaker. On the other hand, section of the splanchnic nerves leads to a hypertonic stomach with shallow contractions, showing an increased rate and tending to run into incomplete tetanus, while complete isolation of the stomach from the central nervous system leads to a hypotonic stomach with about

the normal type of gastric hunger contractions. Somewhat similar changes have been described by Cannon (*30, 33*) on cats, for the digestive movements, and by Carlson (*44*) on dogs, for the movements of the empty stomach.

Although the sectioning of these nerves in various animals has led to certain changes in gastric tonus, as arising from the influence exerted

TABLE V

Effect of section of the vagus nerves on volume capacity
of stomach and contractions

Date 1918	Conditions	Air in balloon	Strength of con- tractions	Remarks
		cc.	cm.	
August 7	Stomostomized	. .	. .	
August 10	Normal....	10	6.5	
August 11	Normal....	10	6.0	
August 12	Normal	10	6.5	
August 13	Vagotomized........	..	...	Operation successful
August 16	Vagotomized........	15	6.5	
August 17	Vagotomized........	15	8.0	
August 18	Vagotomized........	15	6 8	
August 19	Vagotomized........	15	7.0	
August 20	Vagotomized........	15	8.0	
August 21	Vagotomized	15	6.5	
August 22	Vagotomized........	13	6.5	
August 23	Vagotomized........	10	6.0	
August 24	Vagotomized	10	4.5	
August 25	Vagotomized........	10	5.5	
August 26	Vagotomized........	10	5.8	
August 27	Vagotomized........	10	6.2	
August 28	Vagotomized........	10	5.0	
August 29	Vagotomized........	10	4.0	
August 30	Vagotomized........	10	3.5	
August 31	Vagotomized.	10	Very weak	
September 1	Vagotomized	10	Very weak	
September 2	Vagotomized.... ...	..	...	Animal died. Au- topsy showed both vagi cut.

through the extrinsic nerves supplying the stomach, no attempt has been made to analyze the question quantitatively. In order to study the changes in volume capacity of the empty stomach as influenced by partial and complete isolation from the central nervous system, twenty-one animals were used for the various observations recorded herein, as follows: seven were vagotomized, seven splanchnicotomized and seven vago-splanchnicotomized. In addition, fifteen other animals were used but as the length of the duration of these experiments was more or less brief due

to parasitization or other causes leading to an early death, the data from these were excluded. However, in none of these experiments in which results were obtained, were they contradictory to the typical results as tabulated. There were also a few animals of this number excluded because of incomplete nerve section. The following tables have been prepared as showing typical results of the experiments.

TABLE VI

Effect of section of the splanchnic nerves on volume
capacity of stomach and contractions

Date 1918	Conditions	Air in balloon	Strength of contractions	Remarks
		cc.	cm.	
August 7	Stomostomized......	..	...	
August 10	Normal............	10	6.0	
August 11	Normal............	10	6.7	
August 12	Normal............	10	6.5	
August 13	Splanchnicotomized	..	...	Operation successful
August 16	Splanchnicotomized.	4	0.5	
August 17	Splanchnicotomized.	4	1.0	
August 18	Splanchnicotomized..	4	0.8	
August 19	Splanchnicotomized.	4	0.6	
August 20	Splanchnicotomized.	4	0.5	
August 21	Splanchnicotomized.	4	1.4	
August 22	Splanchnicotomized..	6	0.5	
August 23	Splanchnicotomized.	10	0.3	
August 24	Splanchnicotomized.	10	0.4	
August 25	Splanchnicotomized.	10	0.3	
August 26	Splanchnicotomized.	10	0.3	
August 27	Splanchnicotomized	10	0.2	
August 28	Splanchnicotomized.	10	Very weak	
August 29	Splanchnicotomized..	10	Very weak	
August 30	Splanchnicotomized	10	Very weak	
August 31	Splanchnicotomized.	..	...	Animal died. Autopsy showed splanchnics cut.

The animals used for the observations in the preceding experiments were twelve to thirteen inches in length, extended, and it was found, without exception in this size of animal, that 10 cc. of air introduced by a syringe into the gastric balloon was sufficient to maintain a constant manometric pressure of 2 cm. in the stomach of the normal animal. Larger animals, in proportion to size, require greater quantities of air to obtain this constant manometric pressure, and vice versa. In one case, a very large frog measuring sixteen inches, the only one used in the series of experiments, 15 cc. of air were necessary to produce the constant pressure of 2 cm. in the

water manometer. The question of the elasticity of the rubber balloon may arise here for, as Osborne (*161*) pointed out, in thin-walled rubber bags the extensibility of the elastic material is great and its dimensions, including its thickness, alter much under the stretch imposed. Furthermore, a subspherical bag may change in general figure as its size is altered, or changes in the physical consistency of the rubber membrane may result as inflation and deflation proceeds, all of which would lead to serious complication for the analysis of results. However, in the case of the gastric balloon used, 10 or even 15 cc. of air, do not fill the rubber balloon so that the tension of the bag's elasticity complicates the stomach tonus.

In testing out the amount of air necessary to produce the constant manometric pressure, it was found that in all the animals a much smaller amount than 10 cc. of air would produce changes in the manometer amounting to two or more centimeters, but the length of its duration was very short and the pressure soon fell to the zero level or closely approximated it, depending on the quantity of air introduced. This is indicative of the ease with which the stomach adapts its size to the volume of its contents.

In female animals filled with large egg masses, the number of cubic centimeters of air necessary to produce the constant pressure showed no variations from that of the non-egg-carrying female and of the male, although the abdomen was much enlarged. This condition in the egg-carrying female is doubtless accounted for, at least in part, by a reflex mechanism leading to a relaxation of the abdominal muscles, an adaptation similar to the reflex relaxation of the rectus abdominis muscle in increased volume contents of the stomach as has been described by Pike and Coombs (*187*). The animals, with very few exceptions, were run continuously as soon as recovery was complete after the operation, and the fast commenced immediately.

Section of both vagi or the vago-sympathetic nerves in the neck of the frog increases the volume capacity of the stomach temporarily, as shown in table V, from the normal of 10 cc. to 15 cc. of air. This condition invariably lasts from eight to nine days. Usually, on the ninth day following the cutting of the nerves, there is a decrease in the intragastric pressure to about 13 cc. of air; and on the next day it drops again to the normal 10 cc. level and remains there. In other words, the normal tone of the stomach has been reëstablished (Fig. 42), and this condition as it exists in the frog may be comparable to the temporary loss of tonus as described by Cannon (*30, 33*) in cats. The contractions of the empty stomach tend

to approach the normal, but on the whole they are of a slightly slower rate and more irregular. The amplitude of the individual contractions may even appear greater than normal and this may be because the contractions start rather suddenly and without any marked preliminary increase in tonus in the fundic end of the stomach.

TABLE VII

Effect of section of the vagi and splanchnic nerves on volume
capacity of stomach and contractions

Date 1918	Conditions	Air in balloon	Strength of con-tractions	Remarks
		cc.	cm.	
October 22	Stomostomized	..	...	
October 25	Normal................	10	6.5	
October 26	Normal	10	6.5	
October 27	Normal................	10	6.9	
October 28	Normal	10	6.7	
October 28	Vagi and splanchnics cut	..	...	Operation successful
November 2	Vagi and splanchnics cut..	15	6.7	
November 3	Vagi and splanchnics cut..	15	7.0	
November 4	Vagi and splanchnics cut.	15	6.9	
November 5	Vagi and splanchnics cut.	15	7.2	
November 6	Vagi and splanchnics cut.	15	6.6	
November 7	Vagi and splanchnics cut	15	8.0	
November 8	Vagi and splanchnics cut	15	6.5	
November 9	Vagi and splanchnics cut.	15	5.8	Morning
November 9	Vagi and splanchnics cut..	13	6.0	Night
November 10	Vagi and splanchnics cut..	13	5.0	
November 11	Vagi and splanchnics cut.	13	4.4	
November 12	Vagi and splanchnics cut..	13	3.5	
November 13	Vagi and splanchnics cut..	13	3.4	
November 14	Vagi and splanchnics cut .	13	3.5	
November 15	Vagi and splanchnics cut	13	Very weak	
November 16	Vagi and splanchnics cut..	13	Very weak	
November 17	Vagi and splanchnics cut	13	Very weak	
November 18	Vagi and splanchnics cut..	..	...	Animal died. Autopsy s h o w e d both vagi and splanchnics cut

Section of the splanchnic nerves in the frog markedly decreases the volume capacity of the stomach temporarily, as shown in table VI, from the normal of 10 cc. to 4 cc. of air. This marked diminution in size, like the increase after double vagotomy, invariably lasts from eight to nine days. Usually, on the ninth day following the cutting of the nerves, there is an increase in the intragastric pressure to about 6 cc. of air, while on the next day it reaches again the normal, or 10 cc., level and remains there. Here

again the stomach has reëstablished its gastric tonus (Fig. 42)· This condition in the frog is much more marked than Carlson (44) found it to be in dogs. May not the number of motor fibers in the vagi destined for the stomach vary in different animals, as the number of cardioinhibi-
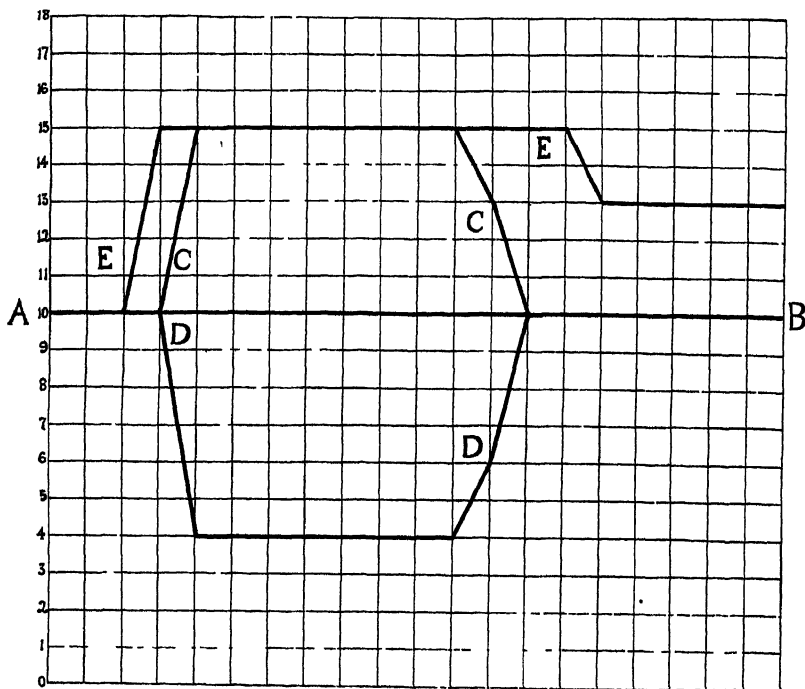
FIG. 42.—The spaces left to right indicate the number of days experiment ran. Vertical spaces above and below the heavy line A B, representing the normal pressure of 10 cc. of air necessary to maintain a constant pressure of 2 cm. in the water manometer, indicate the positive or negative changes from the constant in the volume capacity of the stomach as influenced by the extrinsic nerves. Curve C C, shows effect of sectioning both vagi on stomach. Curve D D, effect of splanchnic section. Curve E E, combined effect of section of both vagi and splanchnic nerves. Note complete recovery of gastric tonus in first two cases, while in the latter there is only partial recovery. Heavy line A B also indicates negative effect of decerebration on stomach. Figures at left indicate number of cubic centimeters of air in balloon.

tory fibers varies in the vagus of the cat and the dog? The contractions of the empty stomach are small, showing an increased rate and a tendency to approach incomplete tetanus. This is especially true during the temporary period of high tonal activity when only 4 cc. of air are required to maintain the constant manometric pressure; and in one animal 3 cc. of air were found to be sufficient. In a few such animals I have found in

the morning, following the removal of the balloon the night before, such strong gastric and esophageal contraction that it was impossible to introduce the balloon through the short esophagus into the stomach without first introducing a small glass seeker, and stretching it. I have even had difficulty in introducing the seeker the first time on one or two occasions because of such marked contraction. This would seem to uphold the views of Cannon (*30, 33*) and Kelling (*109*), that the gastric fibers of the vagi function to make the gastric muscles exert a tension.

Section of the vagi and splanchnic nerves in the frog increases the volume capacity of the stomach permanently, as shown in table VII, from the normal of 10 cc. to 15 cc. of air, but in this case there is not a complete recovery. After this complete isolation of the frog's stomach from the central nervous system, the 15 cc. stomach invariably lasts from twelve to thirteen days, which is a longer period than in either the vagotomized or splanchnicotomized stomach. Usually on the thirteenth day following the sectioning of these nerves, which is accomplished at one operation, there is a fall in the intragastric pressure to a 13 cc. level, where there are no further changes (Fig. 42). This new and partial readjustment of the hypotonic stomach is evidently determined by the intrinsic local gastric motor mechanism of the stomach wall, for the gastric hunger contractions persist after its isolation from the central nervous system. The appearance of the individual contractions is much the same as when the vagi alone are cut. These contractions may exhibit a greater or lesser amplitude and show a tendency toward irregularity. All the animals in the different groups were autopsied to verify, especially, the sectioning of the respective nerves. In a few of these animals in which the heart was still beating regularly the effect of vagal stimulation on the stomach was determined. This resulted usually in a phase of inhibition followed by a stronger phase of excitation immediately upon the removal of the stimulus, and is in confirmation of the findings of Hopf (*94*) on frogs. Stimulation of the sectioned splanchnic usually resulted in a relaxation of the body of the stomach, if any change at all occurred, and if the stimulation was repeated several times in succession it seemed to bring about a constriction of the pyloric sphincter and perhaps also that of the cardiac sphincter, a condition which would seem to indicate that the splanchnics might possess a few fibers of the motor type. The stimulation of these two nerves shows, however, that the fibers of neither have degenerated, and that since the rate of nerve degeneration differs in different animals, and in frogs requires from thirty to one hundred and forty days, depending upon the season of the year (*14*), there is no possibility of the regeneration of these nerves. The

normal functioning of the two sets of nerves to the stomach is indicated by the results of sectioning, as well as by the results of stimulation. In the case of the isolation of the stomach from the influence of the vagi with the splanchnics intact, or vice versa, there is a perfect physiological readjustment of the normal tonus of the gastric musculature. On the other hand, after complete isolation of the stomach (vagi and splanchnics severed) from the central nervous system, there is only a partial physiological readjustment of the gastric musculature. This indicates that the extrinsic nerves play a prominent part in the maintenance of gastric tonus, at least in the frog. When the splanchnics are sectioned it must be the motor fibres of the vagi that produce the high and temporary gastric hypertonicity, i. e., hypertonic stomach. It is reasonable to believe that when the vagi are cut and the splanchnics permitted to exert their full influence on the gastric musculature, these nerves must possess motor fibers—probably to the sphincter muscles—and that these areas then act as tonic rings which, in connection with the intrinsic or local reflex mechanism of the gastric wall, are capable of producing a perfect physiological readjustment. On the other hand, in the case of the stomach completely isolated from the central nervous system, this intrinsic or local gastric mechanism is incapable of bringing about a complete readjustment and in consequence of this it creates a new level of gastric tonus. Thus, every reflex is in its own measure an integral reaction, and is purposive in that it bears some biological purport for its organism. This physiological readjustment occurred regularly in all the animals—that is, it could be looked for after a lapse of a certain number of days following the sectioning of the nerves. For example, in the case of the vagotomized stomach, with this readjustment started, I have seen in a few instances the pressure in the manometer increase from the constant level of 2 cm. to 5 or 6 cm., but I have never observed it in the stomach of the normal animal. In the splanchnicotomized stomach the first readjustment stage is marked by a fall, in the manometric pressure, to zero.

The changes in gastric tonus observed throughout this series of experiments are so slight in the normal frog that they are practically unmeasurable. However, tonus is the prime condition for that tension which must be developed before contraction can result, and if the tension persists the contraction recurs (*32*). Furthermore, the importance of the tonic state in the normal functioning stomach is reinforced by the fact that when all the extrinsic nerves are cut the stomach develops in time, within itself, a tonic state, while the adaptability of the abdominal cavity to the volume of its contents is left to the postural reflex. It has been shown by King and

Connet (*111*) that the rate of the gastric contractions is increased in decerebrate guinea-pigs and that the stomach becomes hypertonic. According to Rogers (*301*) the hyperactivity of the crop of the decerebrate pigeon is inhibited by food and water as in the normal bird, while the writer has found no change in the type of the contractions from the empty stomach of the normal and the decerebrate frog. In order to study the effect of decerebration on the volume capacity of the stomach, observations were made on six decerebrate frogs. The following table has been prepared from a typical experiment.

TABLE VIII

Effect of decerebration on volume capacity of stomach and contractions

Date 1918	Conditions	Air in balloon	Strength of con-tractions	Remarks
		cc.	cm.	
July 26	Stomostomized.........	..	...	
July 31	Normal	10	6.0	
August 1	Normal...............	10	6.5	
August 2	Normal...............	10	6.0	
August 2	Decerebrated 4:15 p.m...	..	...	Operation successful
August 2	Decerebrated..........	10	6.0	Contractions started again at 5:35 p.m.
August 3	Decerebrated..........	10	6.3	
August 4	Decerebrated..........	10	6.0	
August 5	Decerebrated..........	10	5.2	
August 6	Decerebrated..........	..	...	Animal died. Autopsy showed complete re-moval of cerebral hemispheres.

Decerebration in the frog has no effect on either the volume capacity of the stomach or the amplitude of the individual contractions, as is shown in table VIII. There is also no change in the type of contractions. The negative findings in these experiments show that the higher cerebral centers in the frog play no appreciable part in either the maintenance of gastric activity or the tonic state. Since section of the vagi leaves the stomach in a temporary hypotonic condition (15 cc. stomach), while the decerebration effects are negative, we may infer that impulses from centers in the mid-brain and medulla exercise the controlling influence and produce—after section of the splanchnics—the temporary hypertonic stomach, i. e., high gastric tonus. It may be further implied that there is a dynamic readjustment in the central nervous system which leads to an

actual diminution in the inhibitory impulses through the splanchnics after vagal section; or an inverse motor condition existing through the vagi after splanchnic section; or else the stomach may bring about its physiological readjustment by an increased resistance or tolerance of the splanchnic or motor impulses over the respective nerves to the gastric mechanism.

To summarize: The normal stomach of the frog possesses a marked capacity for adapting itself to the volume of its contents with only minimal changes in the intragastric pressure. This is in confirmation of the work of Grey (*89*) and others. Both the intrinsic and extrinsic nerves take part in the maintenance of gastric tonus, as is shown by partial and complete isolation of the stomach from the central nervous system. Section of the vago-sympathetic nerves (double vagotomy) with the splanchnics intact, increases the volume capacity of the stomach temporarily, but there is later a complete readjustment. Section of the splanchnic nerves with the vagi intact decreases the volume capacity of the stomach temporarily, but there is again a complete readjustment, as above. Section of both the vagi and splanchnic nerves (complete isolation of the stomach from the central nervous system) increases the volume capacity of the stomach permanently, and in this case there is only a partial readjustment, at least for a period extending over three weeks, and the tonus of the stomach is established upon a new level from that of the normal. Decerebration affects neither the volume capacity of the stomach nor the type of the contractions.

THE WORK OF THE EMPTY STOMACH OF THE BULLFROG ESTIMATED IN FOOT POUNDS

In this series of studies on the bullfrog it seemed advisable to determine the energy output of the stomach and to estimate it in terms of foot pounds per hour and per day. The animals were prepared by the usual stomostomy procedure and the balloon method was used.

The water in the manometer, plus the float with its writing point, constituted the load (16.9 gms.) moved by the contractions of the stomach. These were carefully weighed daily and any loss of weight due to evaporation of water was made up when necessary to keep the load constant throughout the period of the experimentation. Since the manometer is a U-shaped tube, the distance that the float travels is only one-half the total distance that the load is lifted, so in order to obtain the actual amplitude of any individual contraction, a multiple factor of 2 may be em-

ployed as in blood pressure manometer readings. The contractions were
recorded during hourly periods, the actual height of each gastric contrac-
tion being measured in millimeters, and the total in feet, then multiplied
by 2 to obtain the actual distance the load was lifted or moved, the con-
stant manometric pressure of 1 to 2 centimeters of water being disregarded,

Frog No. 2	Tracing No. 4	Date 7–22–31

63 contractions— height of contractions		Fast period 261 hours
85	97	Load = 16.9 grams.
70	88	1 inch = 2.54 centimeters.
90	99	
99	113	
99	104	611.7
106	131	———— = 240.82 inches = 20.07 feet.
102	97	2.54
117	105	
81	94	16.9 × 20
109	99	———— = 0.596 ounce.*
103	97	567
95	105	
114	99	0.596
100	99	——— = 0.03725 pounds.
71	107	16
109	96	
95	97	2 (20.07) × 0.03725 = 1.495 foot pounds per hour.
121	92	
87	87	24 × 1.495 = 35.88 foot pounds per day.
101	97	
106	96	
105	106	
102	75	
76	76	————
67	81	* To convert grams to ounces multiply by 20 and
70	98	divide by 567 (Handbook of Physiology, Halli-
78	90	burton and McDowell, 18th Edition, 1929).
122	95	
94	97	
121	93	
98	102	
112	———	
	6117 mm.	

since the stomach actually does no external work in maintaining this
pressure, yet it is necessary in order to make the apparatus register.

The contraction of muscle, when loaded, results in a performance of
mechanical work. The external work done is clearly the weight raised
multiplied by the height to which it is raised. Therefore, in order to
obtain the greatest amount of external mechanical work out of a muscle,
its contraction must be opposed by a resistance which shall be great enough

to render the contraction slow, and small enough, especially toward the end of the contraction, not to prevent the muscle from shortening completely. If, therefore, the muscle contracts without lifting a weight, or overcoming any resistance, or if the muscle is in tetanus, no weight is raised and no visible external mechanical work is performed. That internal mechanical work is done is shown by the rise in temperature. This supposition is, however, purely theoretical since the muscle always has to carry its own weight. Therefore, in the case of the smooth muscle of the stomach wall no external work is done in maintaining the constant pressure of 1 to 2 centimeters of water in the manometer (tone base). Aside from the change of form in the muscle, the doing of external work is the most obvious effect of muscular activity. But contraction is attended by other important effects. The ability to do work implies a store of energy. To release that energy chemical change must take place. During contraction, therefore, the muscle is the seat of chemical alterations, and these are oxidative in character. Other phenomena accompanying the contraction of muscle are the development of heat and the production of an electromotive force in the active muscle. In other words, we are up against the difficulty of work in the sense of pure physics and work from the point of view of energy expenditure in the organs. The steady tone of the stomach is, therefore, not work in the physical sense although certainly it requires expenditure of energy to maintain it. On this assumption the tone base is disregarded in the measurements of the individual contractions of the frog's stomach in the calculation of the physical or external work done by this organ in foot pounds.

Hence, by the introduction of a rubber balloon, filled with air and connected with a kymographic system, it was possible to obtain, graphically, a series of gastric hunger contractions from which the actual work of the stomach could be estimated in foot pounds per hour. The mathematical procedure for determining this expenditure of energy from the quantitative measurements obtained is shown on the preceding page, which is representative of a typical protocol.

Throughout the experimentation, the animals were kept in a darkened sink about sixteen inches deep and about twelve inches square. The sink was covered and the room kept as quiet and as dark as possible.

Table IX gives a summary of the protocols obtained from all animals studied. This shows that the work done by the stomach varied from 0.471 to 1.579 foot pounds per hour, while the total daily expenditure of stomach energy ranged from 11.304 to 38.896 foot pounds.

In general, the results obtained indicate that there is a somewhat greater expenditure of energy by the stomach during prolonged starvation than during digestion. There appears to be a more or less definite ratio between the period of starvation and the actual work done, but this relationship is not without exceptions. In the third animal used the

TABLE IX

The work of the empty stomach of the bullfrog, estimated in foot pounds per hour and per day. (Summary of Protocols.)

Date	Frog No.	Tracing No.	Fast in hours	No. of contractions per hour	Total height of contractions in mm. per hour	Work done in ft. lbs. per hour	Work done in ft. lbs. per day	Temp.
7– 3–31	I	1	237	42	2085	.515	12.36	33
7– 6–31	I	2	27	45	4485	1.09	26.16	32
7– 6–31	I	3	29	31	2056	.503	12.072	31
7– 7–31	I	4	53	37	2204	.539	12.936	32
7–10–31	I	5	91	34	2050	.502	12.048	32
7–13–31	I	6	162	30	1930	.471	11.304	30
7–20–31	I	7	336	39	2890	.706	16.944	30
7–21–31	II	1	241	66	5950	1.454	34.896	30
7–21–31	II	2	242	66	5399	1 32	31.68	30
7–22–31	II	3	260	63	5573	1.36	32.64	30
7–22–31	II	4	261	63	6117	1.495	35 88	30
7–22–31	II	5	262	67	5966	1.457	34.98	30
7–22–31	II	6	263	43	3436	.84	20.16	30
7–22–31	II	7	264	53	4729	1.155	27.72	30
7–27–31	III	1	725	60	3959	.967	23.208	30
7–28–31	III	2	745	64	4528	1.113	26.712	32
7–29–31	III	3	766	68	5108	1.248	29.952	28
7–12–32	IV	1	341	56	4420	1.08	25.926	29
7–14–32	IV	2	388	56	4372	1.067	25.624	29
7–14–32	IV	3	389	55	3871	.946	22.707	29
7–15–32	IV	4	412	72	6464	1.579	38.896	29
7–21–32	V	1	482	48	4049	.989	23.736	32
7–26–32	V	2	603	51	4023	.983	23.592	27
7–26–32	V	3	604	58	5032	1.229	29.496	27
7–27–32	V	4	626	42	3856	.942	22.608	29
7–27–32	V	5	627	48	4035	.972	23.328	29
7–28–32	V	6	632	45	4505	1.101	26.424	27

results were not quite up to expectations. The period of starvation was more than twice as long as in either of the first two animals, but the total expenditure of energy was not correspondingly high. It was observed, however, that the number of contractions was greater than in the other two cases—which in itself indicates an increased activity. The interval between the individual contractions appears to become shorter as the

length of the fast increases. It must be remembered in discussing this point that noise, light, etc., invariably inhibit gastric activity. On several occasions there were disturbances that could not have been avoided and these no doubt produced their influence on the sum total of the results. The variation in different animals must also be considered, since it was not feasible to record both hunger and digestive activity on the same animal.

In the case of the animal that fasted for a period of over thirty days, the tracings showed evidence of gastric tetanus due to the extreme hypertonicity of the musculature. This observation has not been observed before by the writer, since the duration of the fast periods were much shorter than this. An extremely long period of starvation is necessary to bring out this effect.

However, additional work on this problem is necessary to confirm the findings herein presented.

THE INFLUENCE OF STIMULATION OF THE SCIATIC NERVE PLEXUS ON THE TONUS AND MOTILITY OF THE BULLFROG'S STOMACH

Many investigators, in studies conducted on the hunger activity of various animals, have devoted much time and energy to an attempt to solve the problem of the nervous control of the gastric motor mechanism. Many animals, both vertebrates and invertebrates, have been employed in these experiments, and the results seem to be more or less dependent upon the position occupied by the animal in the evolutionary scale of development; it is, of course, more specialized and complex in the higher forms.

Numerous variations occur in animals, giving different reactions to the same stimuli according to the class to which they belong. Hence, an attempt has been made to determine the reflex effects on the stomach of the bullfrog from stimulation of the vagus and sciatic nerves, in order that we might have a more correct understanding of the comparative relationship in functional activity between the stomach of the amphibian and that of the higher animals, and especially with that of the monkey. Experiments carried out on the monkey (*179*) showed that when the central portion of the sciatic or vagus was stimulated, it resulted in either an augmentation or an inhibition, depending upon the state of tonus at the moment of the application of the stimulus. A hypertonic stomach became inhibited on stimulation, producing relaxation, while a hypotonic stomach was augmented, causing either a contraction or an increase in the gastric tonus, or both. In further experimentation it was shown

that stimulation of the peripheral end of the vagus produced a similar inhibitory or augmentatory action, dependent upon the degree of gastric tonus. These results are in agreement with those obtained by Carlson, Boyd and Pearcy (*50*) on the reflex control of the cardia and lower end of the esophagus on vagus stimulation of cats and dogs. Laughton (*118*) obtained the same results on cats by stimulation of the dorsal vagus nuclei.

It has been found from previous work on bullfrogs. (*170, 171*), that section of the vagi gave temporary inhibition by way of the splanchnics. There was also a slight loss of tonus but this returned to normal in a short period following the nerve section. Decerebration produced no effect on the stomach contractions (*168*). This is confirmatory with the work of von Openchowski (*234, 235*) and of Meltzer and Auer (*145*), on rabbits, who obtained the same results by stimulation of the sciatic with the vagi intact.

In a further investigation by the writer (*178*) on the influence of the vagi on the motility of the empty stomach of *Necturus,* it was found that either stimulation of the peripheral or central ends of the vagus after unilateral vagotomy produced an inhibition of the stomach movements, the latter reflexly. This reflex was abolished by bilateral vagotomy. Therefore, the action of the vagi on the stomach of *Necturus* was inhibitory—which is a reversal of the vagal action in the bullfrog and other higher animals with the exception of the turtle, in which some inhibitory fibers have been demonstrated by Bercovitz and Rogers (*13*).

Carlson (*47*), in experiments on dogs, found that section of both vagi produced a permanently hypotonic stomach. This differs from the work on frogs (*171*), in that the loss of tonus was only temporary. Cannon and Washburn (*39*) reported a slowing and weakening of the peristaltic movements of digestion after bilateral vagotomy in cats. These experiments were carried out, however, with a view of their effect on hunger peristalsis, so no stimulation was used. McCrea, McSwiney and Stopford (*135*) have cited numerous investigators who reported marked variations in different animals undergoing vagus stimulation. They conclude that additional work is necessary to confirm these experimental findings.

Special technique: The animals used in these experiments were bullfrogs (*Rana catesbiana*).

A stomostomy was made after the usual manner (*168, 169*) and the balloon method was used for recording the contractions of the empty stomach.

After a series of normal contractions were obtained from each animal the cerebral hemispheres were removed, since decerebration produces no effect on the stomach contractions (*108*). The animal was anesthetized and an incision two centimeters long made in the mid-line at the anterior borders of the tympanic membranes, and posterior to the eyes. The skin was held back by a hæmostat, and bone forceps were used to remove the skull bone, care being taken to prevent as much hemorrhage as possible. Small pellets of cotton were used to stop excessive bleeding. All of the cerebral hemispheres were removed back to the optic lobes. After bleeding had ceased, the skin was sutured over the cavity.

Stimulation of the sciatic nerve was accomplished through the plexus in order to eliminate any reflex activity on the lower limb muscles. The right sciatic plexus was isolated by an incision made through the skin about two and one-half centimeters in length and just internal to the right ilium. The connective tissue between the skin and the ileo-coccygeal muscle was incised and the fibers of this muscle separated, which exposed the sciatic plexus lying beneath. The plexus was isolated for its entire length, care being taken to avoid injury to the blood vessels. It was sectioned as far caudalward as possible and a silk thread tied around the end for handling. The left sciatic plexus was then isolated and sectioned through an opening in the opposite coccygeal muscle in order to remove any reflex action on the skeletal muscles of the leg, innervated via the left sciatic. The Harvard shield electrode was employed to stimulate the right sciatic plexus and was held firmly in place by means of a band of skin about one centimeter in width, through which it fitted tightly. The end was carried under the skin to the opposite skin incision to project over the opening in the coccygeal muscle between the right ilium and the urostyle. The end of the electrode was then firmly attached to the urostyle with silk threads and the skin drawn around it and likewise attached. The sciatic nerve plexus was then placed in the electrode for stimulation with a rapidly induced current. The nerve plexus and incision was carefully covered with filter paper and moistened with physiological saline solution to prevent drying. This completed the experimental procedure on the decerebrate animal for sciatic stimulation.

Both the right and left sciatic plexuses were stimulated in these animals but negative results were obtained on the stomach (Fig. 43 A and B). This offers evidence that the afferent sensory fibers of the sciatic do not have any reflex connection via nuclei in the brain controlling the movements of the empty stomach in the bullfrog. In higher animals such

reflexes occur, as has been shown by the writer (*179*) on monkeys, and by McCrea, McSwiney and Stopford (*135*) on cats, dogs, monkeys, rabbits, *et al.* These results on the bullfrog demonstrate that in the simplified nervous mechanism of this animal such highly developed and complicated reflexes do not exist.

<div style="text-align:center">

THE INFLUENCE OF STIMULATION OF THE VAGUS ON THE TONUS AND
MOTILITY OF THE BULLFROG'S STOMACH

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It has been shown by the investigations of Carlson (*44*) and Cannon (*30, 33*) that the vagus exerts a controlling influence over the stomach in the maintenance of tonus, which is necessary for normal, functional activity. Whenever the vagal activity becomes impaired, either in the direction of an increase or a decrease, the gastric motility and tonus are also altered, which in the light of the more recent experiments of the writer on monkeys would have a definite bearing on the type of the muscular response of the gastric mechanism, as influenced by reflex activity from the various sensory surfaces of the body. Therefore, it will be interesting to note, through prolonged fasting in bullfrogs, whether changing conditions of tonus will modify the gastric response in a similar manner as in monkeys.

For vagus stimulation an oblique incision was made through the skin in the region of the neck on the right side of the median line, ventral, after the general method of procedure for the isolation of this nerve already described in a previous section of this treatise—see p. 145. Upon exposure the nerve, which accompanies the blood vessels over the anterior border of the levator anguli scapulæ muscle to which it is bound by connective tissue, is separated and sectioned just below the recurrent laryngeal branch in order to obtain as long a nerve as possible. This is necessary to prevent tension on the nerve when in position in the electrode. A silk thread is tied around the end of the nerve for handling. A transverse slit is made in the skin about one centimeter parallel and anterior to the opening described. It should be just wide enough to admit the Harvard shield electrode, so it will fit tightly in place. It is held securely by silk threads attached to the skin and the electrode. The same technique was employed for isolation and section of the left vagus with the exception that no shield electrode was used, and further, that the incision was closed with sutures.

In a number of decerebrate animals used in this work, the peripheral end of the vagus nerve was isolated and stimulated to determine its
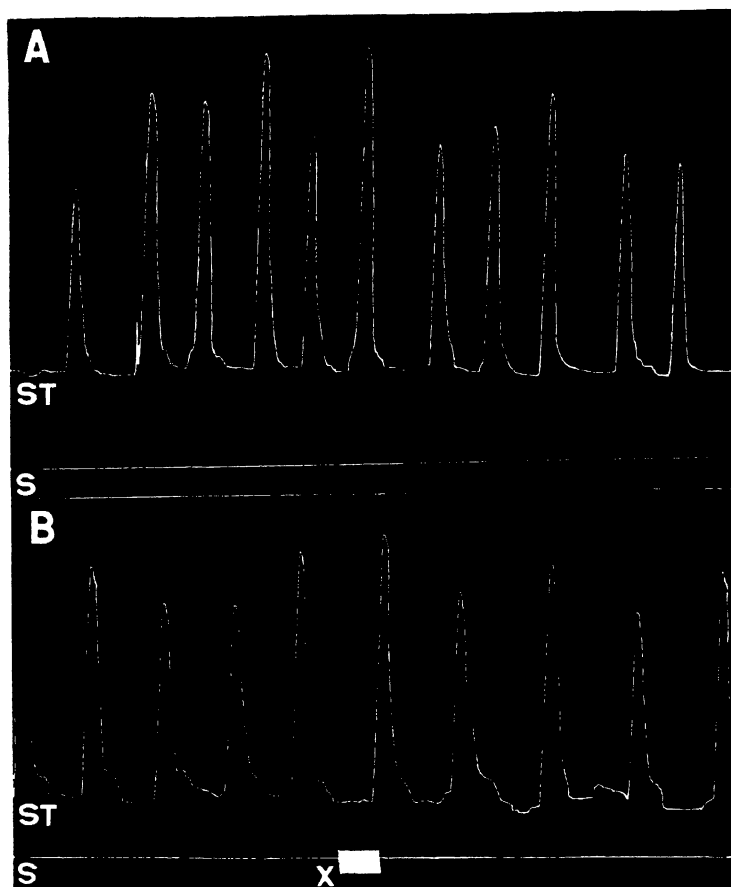
FIG. 43.—A, normal hunger contractions from the empty stomach of Frog III after a fast of nine days. B, hunger contractions from the empty stomach of the same animal after a fast of twelve days and twenty-five hours following decerebration. At x, weak tetanizing current applied to central end of right sciatic plexus, showing total absence of reflex action on stomach. St, stomach contractions. S, signal to indicate zero pressure.

effect on the stomach in situ. In all these experiments on the stimulation of this nerve, there was readily elicited gastric peristaltic activity, which could be observed through the skin and abdominal muscles with the animal lying on its dorsal side. Previous to stimulation the stomach was observed to exhibit no peristaltic movement as recorded by the manometer. This leads us to believe that there are motor fibers to the stomach by way of the vagi, as shown by stimulation of the peripheral end. This is the same result as that obtained by Rogers (*200*) on the
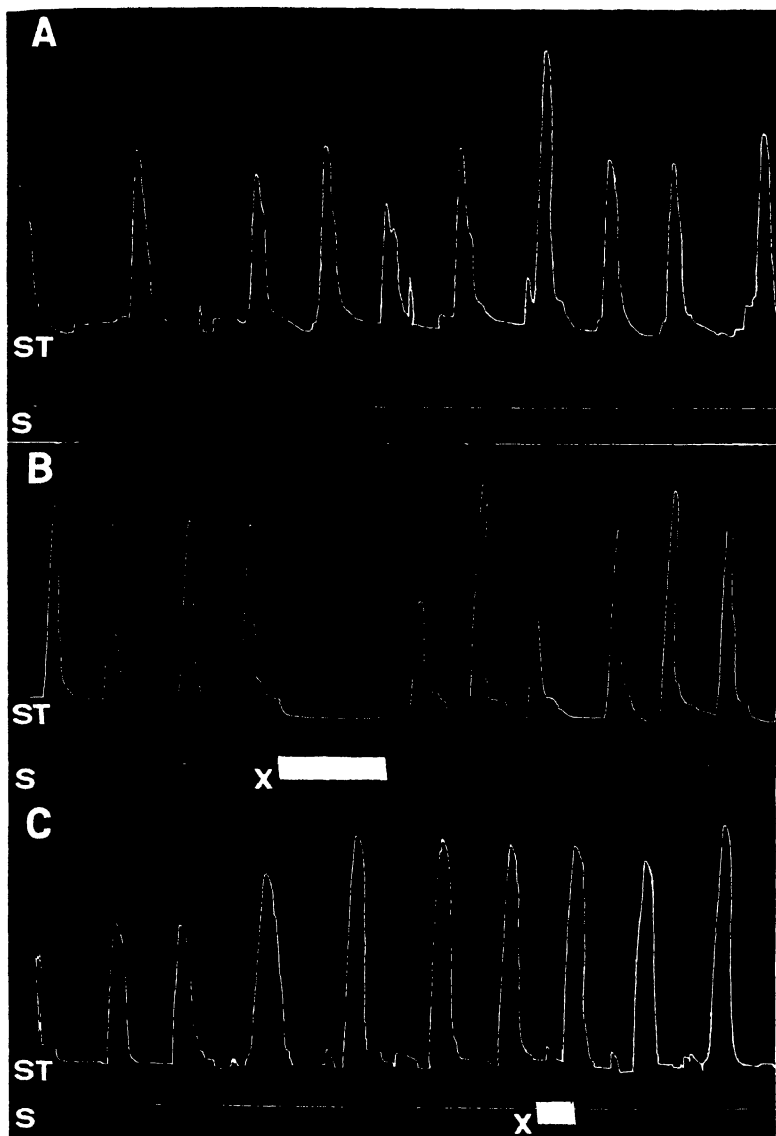
Fig. 44.—A, hunger contractions from the empty stomach of Frog IV after a fast of thirty-five days and fifteen hours following decerebration. B, hunger contractions from the empty stomach of the same animal after a fast of thirty-five and one-half days and twenty-five hours following decerebration. At x, medium tetanizing current applied to central end of right vagus after unilateral vagotomy, producing temporary inhibition of the hunger contractions reflexly. C, hunger contractions from the empty stomach of the same animal after a fast of thirty-six days and forty-one hours following decere-bration. At x, medium tetanizing current applied to central end of right vagus after double vagotomy. Note total absence of reflex inhibition of the hunger contractions. St, stomach contractions. S, signal to indicate zero pressure.

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crop of the pigeon. When the central end of the right vagus was stimulated after unilateral vagotomy it resulted in a reflex inhibition of the stomach (Fig. 44 A and B). This reflex must have been by way of the left intact vagus since bilateral vagotomy abolished it (Fig. 44 C). The same results were obtained on *Necturus,* a low type of amphibian, but the inhibitory effects were even more marked (*178*). Since motor effects were obtained on the stomach from stimulation of the peripheral end of the vagus, while inhibitory results followed stimulation of the central end of the same nerve after unilateral vagotomy, it would indicate that the motor fibers predominated over the inhibitory fibers in the vagus nerve. This would account for the purely motor effects observed on the stomach during peripheral vagal stimulation.

After a prolonged fast of eight hundred and twenty-two hours (five to six weeks) gastric tetany was shown, in which groups of two to four contractions failed to fall to the original base line. This indicates a mild degree of gastric tetany which is present in the stomach of higher animals but which, heretofore, has not been recorded in most lower forms. Slight variations in gastric tonus were demonstrated, especially in cases where there was gastric tetany. Removal of the cerebral hemispheres did not change the type of contractions from the normal.

However, because of the limited number of animals employed in this investigation, the results as yet cannot be considered conclusive.

REPTILIA

TURTLE (*Chelydra serpentina*)

Studies were made on the common snapping turtle (*Chelydra serpentina*) (*168*). In this species the plastron is small and narrow, exposing a great amount of the fleshy parts. It was possible, therefore, to perform a gastrostomy on these animals. An incision about three inches in length was made near the posterior curvature of the plastron of the left side through the abdominal wall, and the ordinary procedure then followed as outlined by Carlson for gastrostomy on dogs (*44*). As a rule, snapping turtles are very vicious (Fig. 45) and are rather unique among chelonians in defending themselves in a similar manner to snakes, that is, by "striking" at the object of anger. The rapidity with which the head is shot forward when these animals are disturbed rivals the dexterity of the rattlesnake, and when we consider that they are provided with a pair

of keen-edged, cutting mandibles and jaw muscles of tremendous power, the stroke of these dangerous brutes may be followed by anything but superficial injury. In fact the amputation of a finger by a medium-sized specimen, or a hand by a very large individual, would be an accomplishment of no difficulty to the reptile (67). Therefore, great precaution must be used in handling these animals for experimental purposes or otherwise. The safest way to handle a large specimen is to pick it up by the tail and hold it well off from the body, but I have found it also quite safe to handle it by the posterior lateral portions of the shell. The animals used weighed from 10 to 15 pounds, and the hunger contractions were recorded by a balloon introduced through the fistula into the stomach. During the recording of the contractions the animals were placed in a specially con-

FIG. 45.—The snapping turtles.

structed box, 17.5 by 10.5 inches and 4.5 inches in depth, and supported on legs 13 inches in height, in the bottom of which was an oval opening 7 inches in length by 4.5 inches in width (Fig. 46). This opening in the bottom of the box gave access to the fistula for the introduction of the balloon into the stomach and removed all possible danger of injury by the animals. This box was provided with a lid at one end covered with wire gauze, and was of such size that the animal was comfortable and could move about slightly, although the internal capacity was not sufficiently large to permit the animal to turn completely around (Fig. 47). With this arrangement the reptile, once it had quieted down, would remain passive for hours, and continuous records of the gastric hunger movements could be obtained with ease. All the records from the turtle were taken on a slowly moving drum revolving at the rate of about fifty minutes per revolution.

THE CHARACTER OF THE MOVEMENTS OF THE EMPTY STOMACH

The gastric hunger movements of the turtle's stomach show an advance in physiological development over the gastric hunger activity of the frog, and conform more to the results obtained from the stomachs of higher animals. In fact, this would be the natural thing for us to expect considering the different positions that these two animals occupy in the ani-
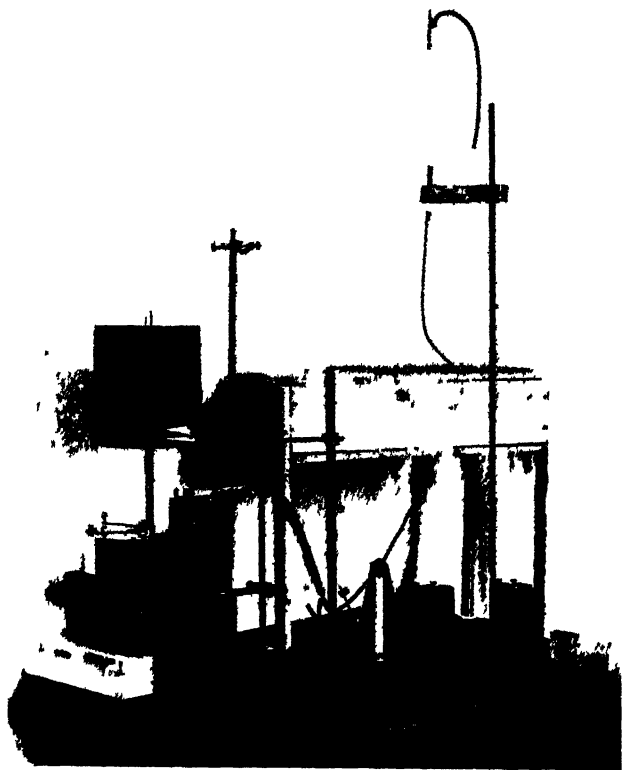
FIG. 46.—The turtle box used during the observational periods.

mal scale. Slight tonus variations are observed and two distinct types of hunger contractions may be described in the turtle. The first type of contraction in this animal (Fig. 48 A) shows an average duration of about one minute, and the intervals between the contractions vary from three to three and one-half minutes. These contractions at first appear to be less vigorous than those from the frog's stomach and perhaps for

this reason they are slightly shorter in duration. This type of contraction is characteristic of the early part of the hunger period and is no doubt analogous to the thirty seconds rhythm in man and dog, Type I contractions. It also corresponds to the type of contractions described for the frog. The small irregular waves which appear here and there in the rest inter-
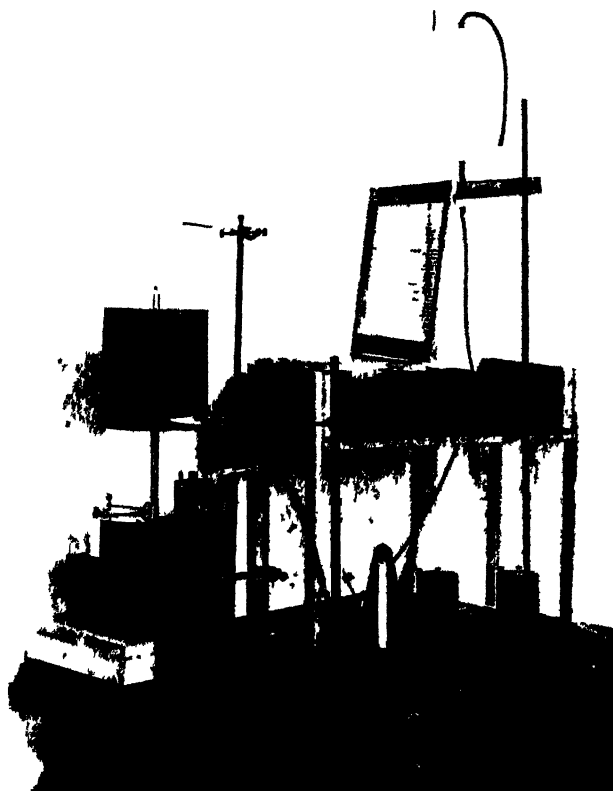
FIG. 47.—The turtle box with side and lid removed to show position of animal. Large oval opening in bottom of box not shown in picture.

vals between the individual contractions are exaggerated respiratory movements. The gastric contraction of the turtle, like that of the frog, is rather moderate in appearance and the curve is perfectly regular with no indication of smaller waves superimposed upon it. In the latter part of the active hunger period the Type I contractions above described gradually change into a second type of contraction which tends to approach
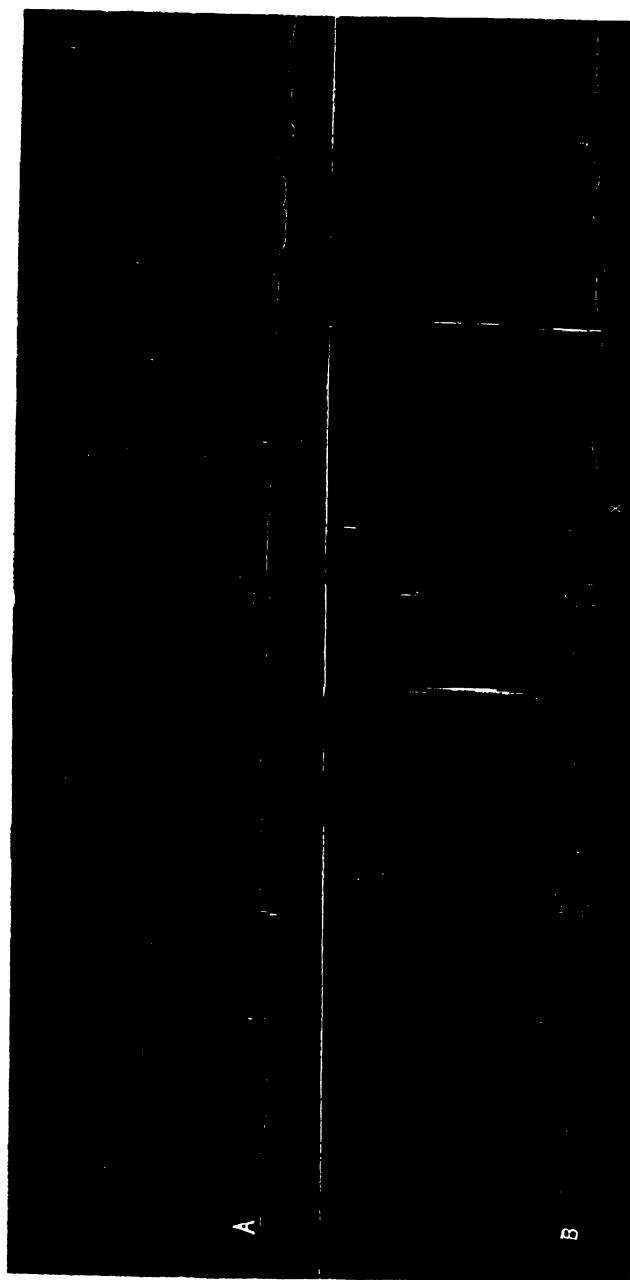
FIG. 48.—Hunger contractions of the turtle's stomach after twenty-one days' fast. A, initial forty minutes of a five and one-half hours' typical period of hunger contractions. B, final thirty minutes of the same active period. At x the active period terminates and the stomach passes into a period of quiescence. Note in tracing B the incomplete tetanus. Water manometer.

incomplete tetanus at every regular periodic contraction of the stomach and this effect becomes more marked as the contractions continue. There is also an increase in gastric tonus during each contraction with its tetany and usually a slight but general increase in the whole tone of the stomach musculature (Fig. 48 B). This second type of contraction is probably the primitive ancestor of the twenty seconds rhythm in man. The contraction with its incomplete tetanus shows an average duration of about two minutes, and the intervals between the contractions in this case vary from three and one-third to four minutes. The hunger contractions of the turtle, unlike those of the frog, but resembling those of the higher animals, fall into groups of gastric activity, separated by intervals of relative quiescence. The duration of the periods of gastric hunger activity vary from five and one-half to six hours and the intervening periods of quiescence of the stomach from one to one and three-quarters hours, with but one exception—in which the quiescent period was found to be of four and one-sixth hours' duration. The period of gastric hunger activity in the adult turtle appears to be relatively long as compared to that of an adult dog (*165*), which ranges from one and one-half to three hours in length; but again, when we stop to consider the place of this animal in the vertebrate scale we should expect it to take an intermediate position and that the gastric activity would also be intermediate between the frog and the higher animals. This is evidently the case. The gastric motor mechanism of the turtle shows a physiological development above the state of a simple, continuous contracting organ so characteristic of the stomach of the frog, yet it has not become sufficiently developed to be classed physiologically with the stomachs of higher animals. Therefore, it must play the important part of a connecting link in the gastric motor mechanisms of animals. The stomach of the turtle, like that of the frog, also exhibits the property of expansion and dilatation as determined by increasing the pressure in the balloon.

THE INHIBITION BY ACID AND ALKALI

Substances introduced directly into the stomach, via a small rubber tube passing through the fistula (water, 1 per cent. sodium carbonate and 0.5 per cent. hydrochloric acid), produce inhibition of the gastric hunger contractions; and the degree of this inhibition is in direct proportion to the stimulating power of the substances introduced. It is most marked in the case of the acid, and least in the case of the water. According to the studies of Thorell (*225*), by the use of adrenaline on reptiles this inhibition would be effected through the action of the sympathetic. In gen-

eral, these inhibitory effects are in accord with those obtained from the empty stomachs of most other animals.   .

In prolonged fasting, the stomach activities in all mammals so far studied are greatly augmented and show without exception marked tonus variations in the stomach musculature. In dogs, during prolonged fasting there is a marked increase in the gastric tonus to within a few hours of the death of the animal, or at least, until that point is reached where the stomach becomes involved in the general debility and cachexia, and this increase in the gastric tonus appears to be directly proportional to the decrease in the amplitudes of the hunger contractions (*166*). In the turtle there are only slight tonus variations while in the frog there are no tonus variations of sufficient strength to be recorded by my apparatus, except in extreme fasting. There is no general increase in the gastric tonus in the turtle in prolonged fasting, but we have instead a marked increase in the amplitudes of the hunger contractions with no appreciable increase in the gastric tonus—as is shown by the accompanying chart (Fig. 49). The same results are indicated in the frog, although this animal was not subjected to such long periods of fasting. These results are just the reverse of what was found in the case of the dog (Fig. 75). The longest fast on the turtle covered a period of sixty-four days, a little over nine weeks, during which time the animal took no food but had access to water except while the stomach records were actually being recorded. However, in the latter part of this fast there probably entered into the work, to some extent, the factor of thirst, since it was found advisable not to change the animal too often from the specially constructed box. The animal at this stage of the fast had become very restless and any disturbance tended to increase the restlessness, which made the record taking very difficult. At about the beginning of the fifth or sixth week of the fast, the turtle became so restless and uneasy that a good tracing could hardly be obtained. This restlessness gradually increased in intensity until about the eighth week, then gradually began to subside until the end of the fast, when the animal had become quite passive again. This indicates that the disagreeable hunger pangs in the turtle probably do not start as early as in the higher animals (*166, 167*) and that it also requires a longer time to fatigue the neurones in the central nervous system, which have to do with the sensation of hunger. This is the result we would rather expect in this low form of vertebrate since periods of enforced starvation are not uncommon among
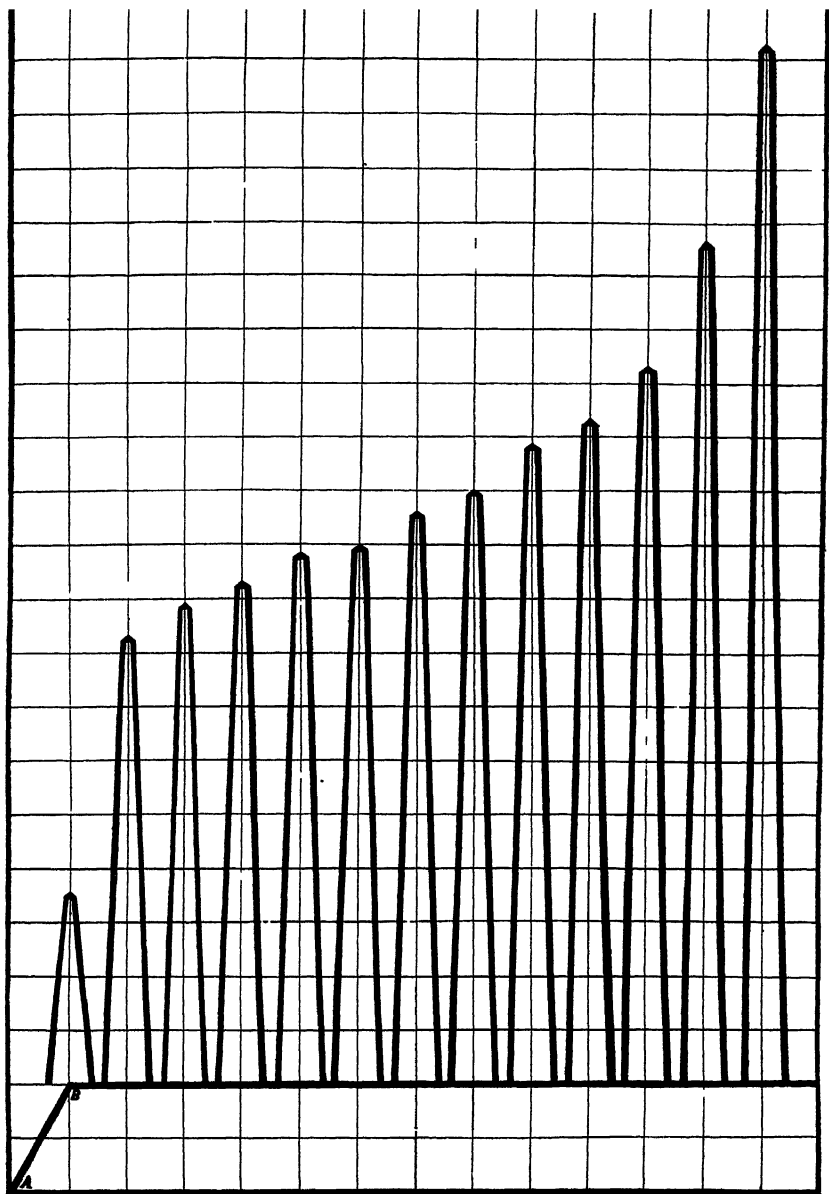
FIG. 40.—Diagrammatic representation of the increased amplitude of contraction on the base of the constant tonus as constructed from the tracings of the turtle on every fifth day. Each of the above squares represents one sq. cm. The erect pyramids indicate the amplitude of the hunger contractions in centimeters arranged on the constant tonus as a base line. Spaces left to right indicate periods of five days' fasting. Heavy line at bottom of chart = 0 mm. pressure of water manometer. A to B = constant pressure of 2 cm. used throughout the experimentation. Note the enormous increase in the amplitude of the hunger contractions at the end of the 64 days' fast.

wild animals.   The amplitudes of the hunger contractions gradually increased with the length of the fast, the contractions became longer and the rate slower.   The contractions, after a nine weeks' fast (Fig. 50), show an average duration of about four minutes and the intervals between the contractions vary from three and one-half to four minutes.   It will be seen from the above that the length of the hunger contractions under these conditions has been increased from two to four times.   It is also of interest to note the ease with which these enormous hunger contractions are inhibited by forced respiratory movements, even at the time of the onset of one of these very strong contractions, as in B (Fig. 50).   These respiratory movements or sighs are also exaggerated in prolonged fasting and during each of them the animal usually gives a hissing sound.
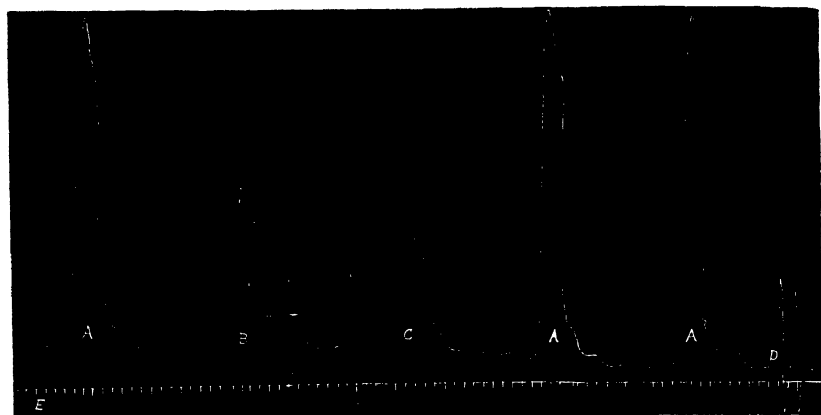
Fig. 50.—Hunger contractions of the turtle's stomach after nine weeks' fast. A, normal contraction. B, inhibition of the very strong hunger contraction by the respiratory movement, D, with recovery through C. E=time in 30 second intervals. Water manometer.

THE EFFECTS OF SEASONAL VARIATIONS ON THE GASTRIC HUNGER ACTIVITY

The effects of seasonal variations are well illustrated by the turtle. Records of the gastric movements have been taken through the changes in the seasons from August, 1915, to May, 1916, inclusive.   In all instances the activity of the gastric motor mechanism followed the climatic changes in temperature (Fig. 51).   In the coldest days of winter, when the turtles showed little or no gastric activity, placing the animals in a tank of warm water for half an hour would greatly augment the gastric movements. However, the gastric hunger movements in winter are never as vigorous as in summer, as is shown by my series of experiments.   During the winter the turtles took no food, although it was offered to them many times.

In conclusion, the hunger contractions of the empty stomach of the turtle are very similar to those of the bullfrog. The rate of the contractions is somewhat less, and there are periods of relative quiescence of the empty stomach, similar to that in mammals and birds. In prolonged starvation the contractions become stronger and show a tendency to pass into short periods of incomplete tetanus.

<center>AVES</center>

<center>PIGEON (*Columba* sp.)</center>

The most recent work on the digestive apparatus of birds is that of Reed and Reed (*194*) on the mechanism of pellet formation in the great
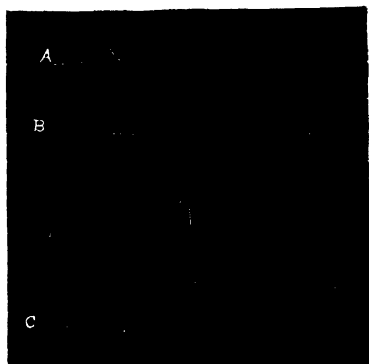
FIG. 31.—Gastric hunger contractions of the turtle at different seasons of the year. A, contractions on a moderately cold day in winter (January). B, contractions on a very cold day in winter (January). C, contractions two and one-half days after the break of winter (March 28), weather mild and warm.

horned owl, *Bubo virginianus,* but these investigators made no observations on the gastric motility of this animal.

The author (*177*) has repeated the experiments of Rogers (*201*) on the pigeon and both agree that the contractions of the empty crop of this species of bird may be studied either by the balloon method or by direct observation. In the normal bird these contractions are not easy to demonstrate except by the balloon method, since the hungry animal in a cage is in a state of restless excitement, in which it can be seen only that the crop is empty. If such a bird is quieted, however, in a partially darkened cage, with the observer sitting quietly at the side, the contractions of the empty crop can be seen without any form of registering apparatus. This demonstrates that the presence of the balloon in the crop does not necessarily act as the stimulus to the contractions, and overcomes the objection of some to the balloon method for this type of

work. The failure of Rossi (*205*) and Doyon (*70*) to control the in-
hibitory influences is probably one reason for these investigators claim-
ing that the empty crop is quiescent. The placing of blinds over the
bird's eyes usually has the same quieting influence as darkening the cage.
Under these conditions, with the bird quiet, one is able to observe at
intervals one or more deep peristaltic waves running over the entire crop;
and this is frequently the precursor of the bird becoming restless. At
other times, instead of the periodic contractions the entire crop may be
so constricted as nearly to obliterate its lumen. This indicates that
there is a relation between tonus and distension as described by Cannon

FIG. 52.—Dorsal aspect of head
of pigeon after bone excavation
and removal of cerebral hemis-
pheres. Note the size and posi-
tion of the bone openings, the
bridge of bone in the center pro-
tecting the median sinus and the
mid and hind brain showing within
the posterior portion of the cavity.

(*33*) for the mammalian stomach, since peristaltic contractions will not
appear on such a constricted organ. Between this high degree of con-
striction and that of a partially relaxed crop over which run deep peri-
staltic waves, there may be found all intermediate gradations in the same
bird at different times.

The preceding facts which with patience can be observed in the normal
bird are more readily demonstrated in the decerebrate animal, for here
the inhibitory influences are at a minimum. The behavior of the crop
of the operated bird is practically identical with that of the normal,
with the exception that the gastric activities are no longer related to dis-
tant influences.

The procedure involves etherization of the bird and surgical removal
of all the forebrain anterior to the thalamus. Elaborate aseptic pre-
cautions are unnecessary in pigeons. The chief difficulty is in removing

all of the forebrain without causing injury to the thalamus and cerebellum or injuring the cerebral circulation. The technique employed after etherization, consists of clipping the feathers from the top of the head and exposing the cranium by a longitudinal incision through the skin. With a scalpel, a small opening is drilled through the bone on each side overlying the cerebral hemispheres of sufficient size to admit the point of a scissors blade, and the bone is then carefully removed, with the exception of that portion directly over the median sinus. The dura should not be torn during this process. With fine pointed scissors an incision is
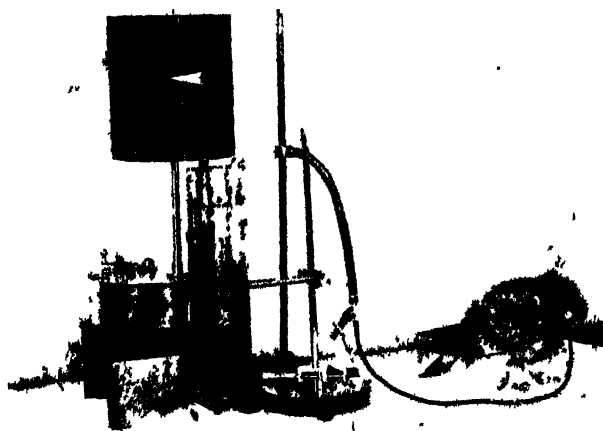
FIG. 53.—Typical decerebrate pigeon, feathers raised, head drawn into shoulders, eyes closed, with balloon in crop connected with registering apparatus.

then made through the dura, over both hemispheres. All this can be done practically without bleeding. A probe with the point curved to fit the posterior border of the cerebrum is then introduced under the dura and the brain substance removed, one side at a time, while the dura is left intact. Hemorrhage is controlled by gently packing with cotton. When the bleeding subsides, the cotton is removed, leaving the cavity empty, and the skin is sutured over the bridge of bone which protects the median sinus (Fig. 52). A thin coat of collodium over the incision completes the procedure.

A fistula is now made in the crop directly following the decerebration and before the animal recovers from the anesthetic. The procedure consists of clipping off the feathers close to the skin from the lower end of the neck and the upper part of the breast. A small incision is made through the skin and the muscularis of the crop. This incision forms the fistula into which is inserted a piece of soft rubber tubing about two inches in length and one-quarter of an inch in diameter, the tubing being slightly larger than the opening, thus putting the tissue around the fistula on the stretch and making secure the tube. No sutures are required. The crop end of the tube is cut obliquely while the exterior end is closed with a cork which is made secure by a safety pin. This also prevents the tube from being drawn into the crop. If the tube is removed the fistula will close in two or three days and the animal is none the worse for the operation. Direct observation shows that such fistulæ do not modify, or only vary slightly, the normal movements of the crop. In twenty-four hours the fistula tube may be removed and a rubber balloon introduced into the crop and connected with a water manometer for graphic registration of the movements (Fig. 53). A balloon about 4 by 4 cm., of the condom type, is used and is tied with a silk thread on to the end of a flexible rubber tube about 4 mm. outside diameter, which contains a small metal or glass cylinder about 8 mm. in length and of such a size as exactly to fit into the lumen of the tube.

THE CHARACTER OF THE MOVEMENTS OF THE EMPTY AND FILLED CROP

The gastric apparatus of the pigeon is anatomically divided into three parts: crop, usually considered as a simple dilatation of the esophagus and similar in structure to it (24), the proventriculus or glandular stomach, and the gizzard or muscular stomach. All parts of this apparatus exhibit motility and, according to Kato (107), the pressure exerted by the contractions of the gizzard during hunger are greater than those occurring after feeding. These contractions may be obtained by simply pushing the balloon into the gizzard through a fistula made in the mid-line of the crop. From the standpoint of comparative anatomy, the crop of the bird may also be considered to correspond to the cardia of the stomach of higher animals.

The hunger contractions obtained from the empty crop, like those obtained from the gizzard in fasting, are more vigorous than the digestive peristalsis after feeding. The hunger contractions of the empty crop exhibit a definite periodicity characteristic of the behavior of the empty

stomach of higher animals (Fig. 55). Sometimes the contractions are rapidly and continuously repeated for several hours, but they usually occur periodically in groups. On the contrary, the movements of the filled crop are of less amplitude, more irregular, and less indicative of a definite periodicity (Fig. 56). After feeding, the hunger contractions are usually entirely absent for thirty to forty-five minutes. Then, at short intervals, irregular contractions begin; after an hour or two they gradually increase in frequency and vigor, first appearing in groups of
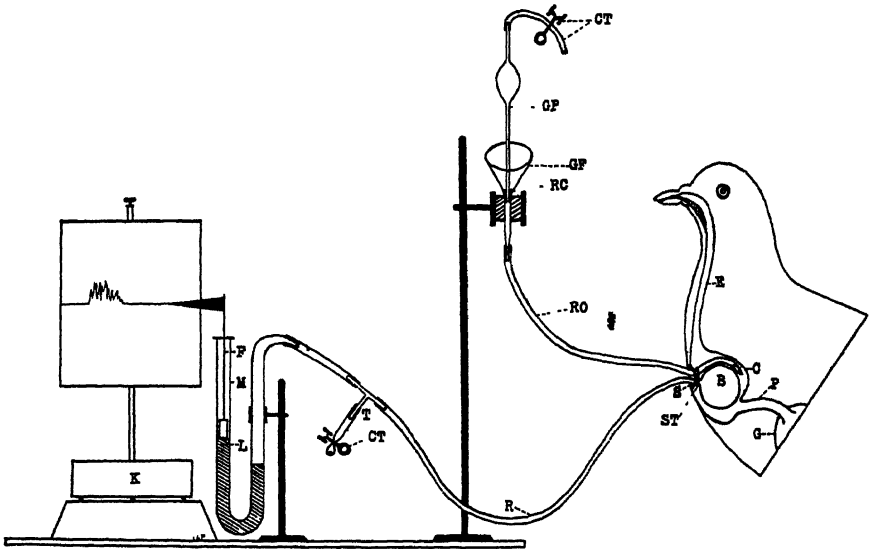
FIG. 54.—Diagram showing method of recording peristalsis of crop of pigeon. K, kymograph. F, glass float with recording flag. M, manometer. L, manometer liquid (water). T, glass T-tube, for inflation of balloon. R, rubber tube connecting balloon with manometer. S, crop fistula. B, rubber balloon in crop. E, esophagus. C, crop. P, proventriculus. G, gizzard. CT, clamp and rubber tube. GP, glass pipette. RC, rubber cuff on end of pipette. GF, glass funnel. RO, rubber tube with open end in crop. ST, silk thread holding tubes together.

three or four waves and then after five or six hours in groups of six to twelve or more, separated by intervals in which the crop is comparatively at rest. It requires from ten to twenty seconds for each peristaltic wave of the empty crop to complete its cycle, whereas the more rapidly repeated contractions of the lower part of the crop occur at the rate of eight to ten per minute. If the bird sets up a struggling sidewise movement it indicates overdistension of the balloon or that the balloon is too large. It has then become a source of irritation. Sometimes a similar condition results from overdistension of the crop with food.
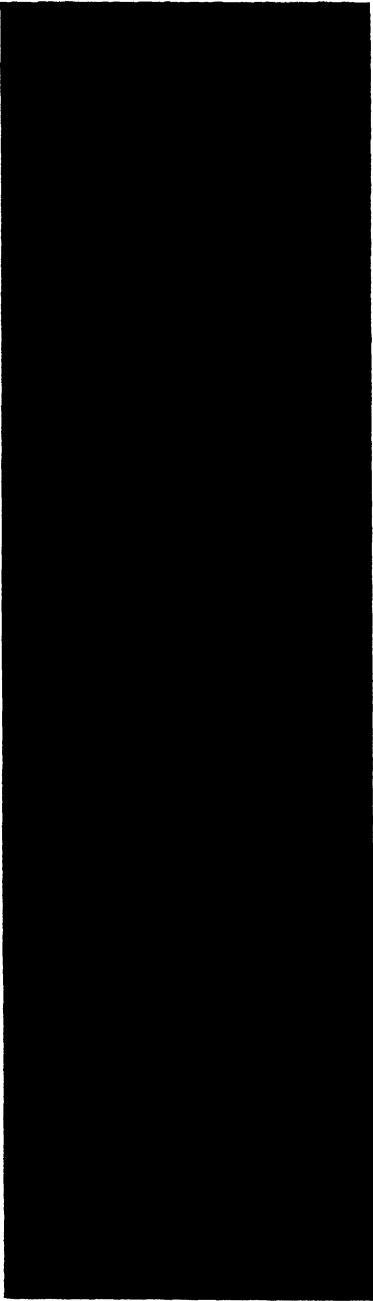
FIG. 55.—Decerebrate pigeon. A, peristaltic contractions of crop twenty-four hours after feeding, crop empty. Note the periodicity characteristic of the behavior of the empty stomach of higher animals (hunger peristalsis). B, time in five second intervals. Water manometer.

FIG. 56.—Decerebrate pigeon. A, digestive peristalsis of crop thirty to forty-five minutes after feeding. Food in crop. B, time in five second intervals. Water manometer.

THE INHIBITION OF THE GASTRIC MOTILITY

For studying the influence of inhibitory substances (liquids) on the movements of the empty crop or the stomach of other animals, a second rubber tube is attached to the basal portion of the balloon tube, with a silk thread with its open end extending to the mid-portion of the balloon. The other end of the tube is connected to the stem of a small glass funnel which has been heated and drawn out to fit the tube. Within the funnel, a pipette with a tapering end fitted with a rubber cuff fits tightly into the opening of the funnel stem. A rubber tube and clamp completes the pipette, so that any desired fluid may be retained therein until the desired moment, when by releasing the clamp it may be permitted to flow slowly through the tube and directly into the crop (Fig. 54). In the case of water there appears to be some quantitative relation between the
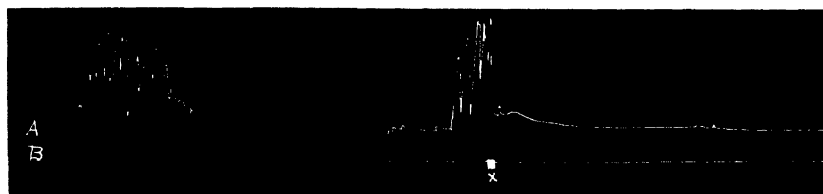
FIG. 57.—Decerebrate pigeon. A, hunger contractions of crop thirty-two hours after feeding, crop empty. B, signal magnet. At x, 8 cc. water at room temperature was introduced directly into crop. Note the abrupt termination of the period of hunger activity, inhibition. Water manometer. (Tracing reduced about one-half.)

volume of fluid introduced and the relation of tonus. Thus 2 to 4 cc. of water does not always produce this inhibitory action while 8 to 12 cc. is effective (Fig. 57). More recently, the author has found, as stated elsewhere in this paper, that very small amounts of food given to monkeys do not lead usually to gastric inhibition, while larger quantities prove effective. In cases where a study of inhibition is desired a larger fistula should be made in the crop and a rubber tube one-half inch in diameter inserted to keep the fistula open.

It is therefore possible to utilize to advantage the decerebrate pigeon for a study of peristalsis, since removal of the cerebral hemispheres does not materially affect the peristaltic movements of the crop. This animal is even more suitable for use in the general student laboratory for such a study than the bullfrog, since decerebration transforms the nervous active bird into a stupid, lethargic creature which reacts only when stimulated. Hence, the bird, in addition to exhibiting the classical effects of decerebra-

tion, may be satisfactorily utilized even under the disturbing influences of the student laboratory for a study of peristalsis. In larger animals, such as dogs, with gastric fistulæ a study of peristalsis can be made only after a period of intensive training and under the quietest surroundings.

MAMMALIA

GUINEA-PIG

The guinea-pig also feeds at frequent intervals and the stomach is never found empty under normal conditions. Observations made by King and Connet (*111*) on this animal, by the fistula and balloon method, have revealed that the mild peristaltic waves of digestion be-
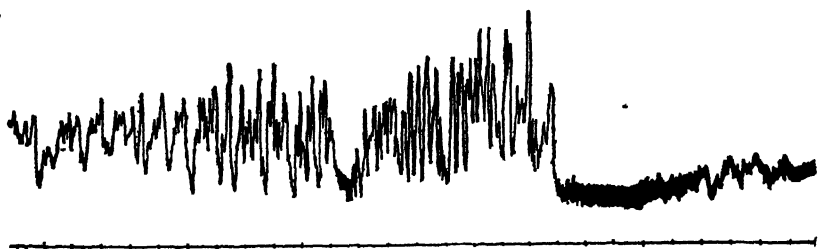
FIG. 58.—Contractions of the guinea-pig's stomach, showing the termination of a period of hunger activity, five hours after feeding. Note the gradually increasing strength of the contractions and the incomplete tetanus terminating the period. Three hours later, when the balloon was removed, the stomach contained food. Time in one second intervals. (Courtesy of Professor Jessie L. King, Goucher College.)

come more and more intense until contractions such as might be classified as Type I hunger contractions occur. This type may continue for four hours, but they gradually merge into the more vigorous Type II and possibly Type III contractions, separated by periods of relative quiescence (Fig. 58). Substances like water, weak acids, etc., which usually produce inhibition of such contractions, give negative results whether swallowed or placed directly in the stomach. After eating, the vigorous movements continue from thirty to sixty minutes and then merge into those of the mild peristaltic type.

Decerebration results in the stomach producing contractions of a similar character with a marked increase in the rate, the stomach being in a hypertonic condition. It is believed that the absence of inhibitory impulses from the cerebral cortex accounts for these striking variations, the positive influence of the brain on the stomach motility originating below the cerebrum.

RABBIT

Rogers (*200*) made gastric fistulas in rabbits by opening the abdominal cavity about one inch to the left of the mid-ventral line and as close to the costal border as possible, suturing the muscularis of the fundic portion of the stomach to the peritoneum and oblique muscles and the gastric mucosa to the skin. These fistulas were made rather small so that there would be little leakage of gastric juice or loss of ingesta. The balloon method was used. The rabbit, like other herbivorous animals, feeds at frequent intervals, and under normal conditions the stomach is never
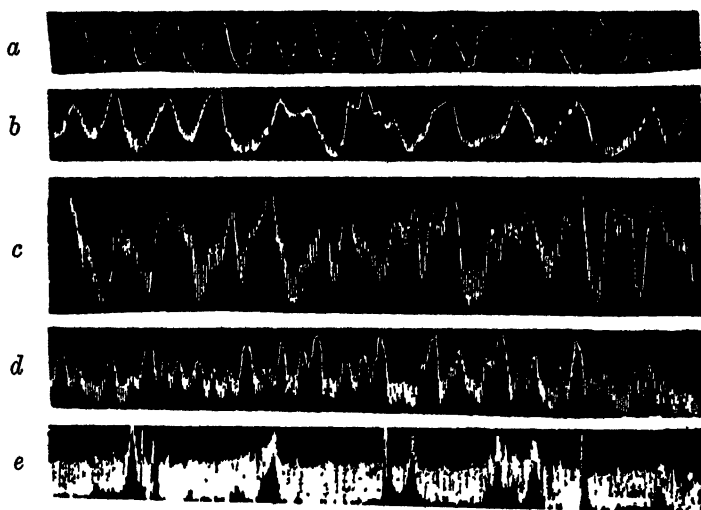
FIG. 59.—Contractions of the rabbit's stomach. *a*, normal digestive peristalsis: *b*, after 24 hours' starvation; *c*, after 75 hours' starvation; *d*, after 92 hours' starvation; *c*, after 110 hours' starvation. The animal died a few hours following the recording of the last tracing. (Courtesy of Professor F. T. Rogers, Baylor University Medical School.)

found empty. In no case did any animal survive a period of continuous starvation of more than seven days and in all such cases there were considerable amounts of moist residue in the stomachs, at death, which ranged from 8 to 13 grams. Normally the moist contents of the adult rabbit's stomach weigh 90 grams or more. The animal, soon after being deprived of its usual food, provides a substitute by eating its own excreta.

Since normally the rabbit's stomach is never empty, it is to be expected that gastric digestive peristalsis will always persist. However, as the period of starvation is prolonged, the stomach contractions are

altered. Instead of being the gentle peristalsis of normal digestion, they become relatively powerful contraction waves which rapidly follow one after the other with a tendency for each peristaltic wave to pass into a short period of tetany. During hunger the strength of these contractions is accentuated, there being no indication of rest or periodicity until a short time before death from starvation (Fig. 59 *a. b, c, d* and *e*). These findings are in general agreement with those of Schalk and Amadon (*209*) on the goat.

Gastric tonus variations were observed more frequently during hunger than during digestive peristalsis. It is suggested that the increasing muscle tone of the stomach, as starvation is prolonged, may play a part in causing the sensation of hunger.

It is also interesting to note that the sight, smell, taste, or chewing without swallowing, of various foods, do not inhibit the hunger contractions. This is in striking contrast to the ease with which similar substances will produce gastric hunger inhibition in man, monkey, dog, etc.

SHEEP

Mangold and Klein (*131*) have made studies on the motor phenomena of the four divisions of the stomach of the sheep, particularly as influenced by the vagi and splanchnic nerves, by the method of direct inspection after opening the abdomen (Fig. 60). Chronic experiments were made with section of the various gastric nerves. The most striking new result reported is that section of the left vagus produces no disturbance of the gastric motor function, while section of the right vagus causes death from starvation through persistent pylorospasm. The right vagus carries predominantly inhibitory fibers to the pylorus and in the absence of this inhibitory tonus the motor tonus of the splanchnic nerves maintains a persistent tonus so great that the animal dies of starvation. Either vagus alone suffices to maintain rumination, while section of both vagi destroys it. The sympathetic nervous system is evidently incapable of maintaining this process.

Magee (*245*) has also studied the nature of the nervous control of the fore-stomachs indirectly by observing the effects on the reticular contractions produced by drugs having an influence on the parasympathetic nervous system. Atropine and amytal, which block impulses via the vagus, slowed the contractions, while pilocarpine, which intensifies vagal activity, caused tetany of the reticulum. Adrenalin, which induces sympathetic effects, slowed the contractions. This investigator, therefore,

concludes that the vagus in general supplies the motor and the splanchnic the inhibitory impulses to the fore-stomachs.

Furthermore, Magee (*245*) has made X-ray studies on the development of the fore-stomachs of a lamb and a young goat at intervals from the age of 3 weeks until the viscera attained adult form. He found that the stomach of the very young animal (3 weeks) was of the simple type, which exhibited a distinct peristalsis in the pyloric region. At the end of the first month, a small shadow appeared near the esophageal opening and anterior to the abomasum, which was taken to be the reticulum. At the end of the second month, this pouch became more discernible and at three months a further fluid level was distinguished with a gas bubble on
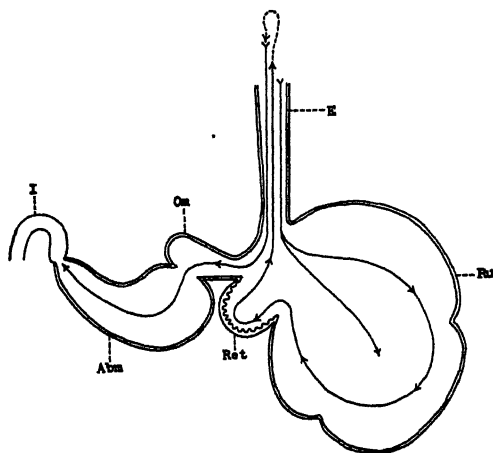
Fig. 60. — Diagrammatic representation of the stomach of a ruminant. E, esophagus; Ru, rumen or paunch; Ret, reticulum or honeycomb; Om, omasum or psalterium; Abm, abomasum or rennet; I, intestine. The arrows indicate the course of the food substance through the stomach, including the process of rumination or the remastication of the ingesta.

top situated dorsal to the abomasum. This sac was taken to be the rumen. As age advanced, the reticulum and rumen became more and more obvious, until at about the seventh month the adult form appeared. The first three pouches of the ruminant's stomach have their origin from the caudal end of the wall of the esophagus. These pouches are rudimentary at birth and during nursing life; but they develop rapidly after the animal begins to eat coarse fodder. A further consideration of the movements of the divisions of the stomach of the sheep and goat will be found in the following section on the goat.

GOAT

Like the stomachs of other herbivora in general, the stomach of the goat is probably never completely empty of food, digestion being more or less of a continuous process. Preliminary studies on the rumen, which

biologically corresponds to the cardiac portion of the stomach of other mammals, have been reported by Schalk and Amadon (*209*), using the gastric fistula and balloon method. The body of the rumen exhibits strong periodic contractions, independent of those concerned with the regurgitation of the food bolus into the mouth, i. e., the act of rumination (Fig. 61 [1]). These contractions differ from those reported on the horse by the same observers and on man, monkey, dog, etc., in not exhibiting periodic activity. In other words, the contraction periods which alternate with the quiescent periods in the animals mentioned above are entirely lacking in the goat. The contractions vary in intensity and appear to be practically continuous, and they occur when the rumen
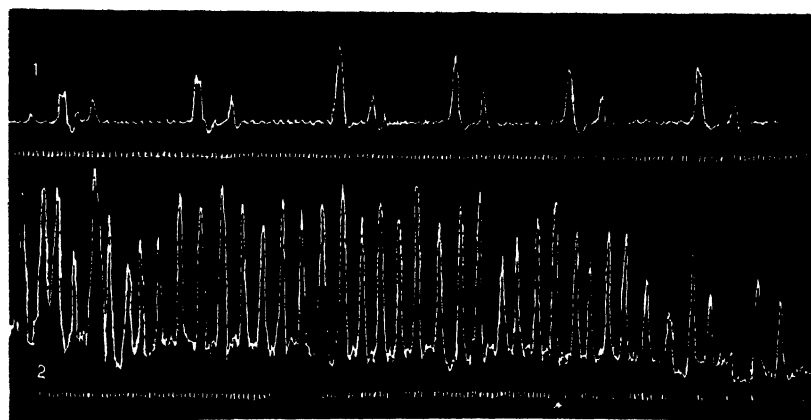
FIG. 61.—1, Normal rumen peristalsis of the goat. 2, eating oats. Finished eating at point marked by arrow. Note the rapid, powerful feeding contractions. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

is partly empty and the animal is manifesting external symptoms of hunger, such as restlessness, etc. When the animal is fasted for several days, or the greater part of the ingesta is removed in the rumen through the fistula, these contractions become stronger without much change in rate. The motor conditions in the goat are essentially similar to those found in the rabbit and guinea-pig. The digestive contractions of the filled rumen pass gradually into the stronger contractions of the empty or partly empty rumen and these latter are provisionally called the "hunger contractions," assuming that it is the partly empty rumen that gives the impetus to feed (Fig. 61 [2]). The only apparent difference between the completely filled and the partly empty rumen is the difference in

tonus and strength of contraction. The feeding response is similar to that found in the stomach of the horse.

Furthermore, the observations of Magee (*245*) on the movements of the different compartments of the stomach of goats and sheep of varying ages by means of X-ray studies of the movements of large opaque $BaSO_4$ and $CaSO_4$ pills (about one centimeter in diameter), which were of varying specific gravity, have given us important facts in determining the rates of contractions of the gastric viscera and the range of movement undergone by the ingesta. However, this investigator found that the changes in shape which the different divisions of the complex stomach of the ruminant assumed could be better studied by the administration of opaque meals. The opaque pills were of particular advantage in studying the contractions of the rumen and reticulum since they were very hard, and if they remained in these compartments, they were found to resist fermentation changes for periods up to 14 days. Heavy pills generally entered the reticulum immediately, where they remained for periods up to 9 days, while light pills, when they entered the reticulum at first, did not remain for more than about 30 minutes, the length of their stay in this sac being dependent on the specific gravity of the pill; the higher the specific gravity, the longer they remained. Sooner or later, however, they were shot rapidly into the rumen, where they moved about for a variable time before entering the omasum. Rumination increases the rapidity of the reticular movements and makes them more extensive.

The reticular movements in the adult animal were found to be very constant, often varying by no more than ± 5 seconds, during a period of 5 hours. In different animals the interval varied from 40 to 80 seconds, and it was not appreciably influenced by periods of fasting up to 48 hours. Fasts of longer duration, however, appeared to affect the frequency. Emotional states slowed the rate, as exhibited in animals unaccustomed to the experimental procedure, so that intervals of several minutes might be observed. In immature animals the contraction rate was slow, but it increased with growth and the results from a young goat gave the mean intervals for the following ages to be—4 months, 90 seconds; 6 months, 75 seconds; 9 months, 40 seconds.

The omasal relaxation, which probably occurs at the height of the reticular contraction, results in a fall in pressure from the reticulo-rumen to the omasum, thus permitting the onward passage of ingesta from the former to the latter compartment. This is probably due, chiefly, to an aspiratory act on the part of the omasum. It is followed by a slow but powerful contraction of the omasum, which doubtless squeezes the fluid

into the vestibule and thence into the abomasum, the solid material being at the same time trapped between the laminæ of the omasum. In the absence of a sphincter at the omaso-abomasal orifice some other mechanism must function to protect the abomasum against overfilling, and Wester (*249*) has shown that pressure in the omasal vestibule inhibits the contractions of the other fore-stomachs, and it is likely, as Wheelon and Thomas (*250*) found in man, that duodenal distension inhibits the pyloric contractions. Furthermore, it is thought, that the variations in the rate of contraction of the reticulum and rumen are probably to be
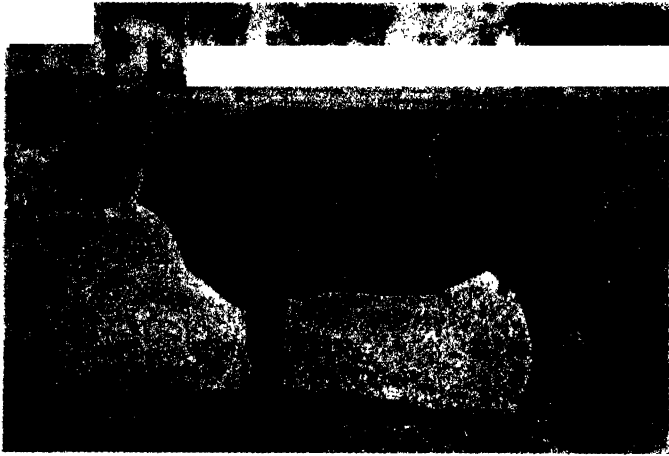
FIG. 62.—An ideal gastric fistula in a cow, several months after operation. Note the smooth skin-rimmed border of the fistula and the normal condition of the animal. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

accounted for by impulses of different intensity emanating from the intestine and abomasum.

The abomasum is lined with glandular epithelium and is, therefore, the homologue of the stomach in man. Its pyloric portion is tubular and at its exit into the duodenum there is a well-developed sphincter. X-ray observations showed this division of the ruminant's stomach to exhibit typical peristaltic contractions in its pyloric portion, and it was assumed, that feebler contractions, probably of a tonal type, were present in the fundic or upper portion of the abomasum. It is believed, as in the case of the human stomach, that the chief objective of the fundic movements is to maintain a more or less constant pressure on the ingesta so that the pyloric portion is kept full.

Magee (*245*) also found that the blood sugar in fasting animals varied from 63 to 86 mgm. per 100 cc. and that it rose steadily from the 40th to the 169th hour of fasting. He also observed that the forestomachs contained food after 7 days' fasting, which would indicate that fermentation of carbohydrate material was going on during this period. Furthermore, the percentage increase in blood sugar after carbohydrate meals was found to be greater in fasted than in the non-fasted animals.

Ox

Rumination, or the remastication of food, is an interesting and radical departure from the ordinary phenomena attending the digestive process

Fig. 63—The cow, with rubber balloon in stomach connected with resistance and recording manometers used for kymographic registration of the gastric motility of different divisions of the bovine stomach. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

in most types of animals. The stomach of the ox is morphologically a very voluminous organ that has a capacity of 20 to 40 gallons, depending upon the size of the animal. It is compound in type as is true of the gastric apparatus of all ruminant animals. Four distinct cavities or compartments are present, which are known as the reticulum, rumen, omasum and abomasum (Fig. 60). The first three are proventriculi or dilations of the esophagus, and their mucosa does not secrete any digestive fluids.

The abomasum is the true stomach where the mechanically prepared food materials first meet the solving action of the digestive secretions. The rumen forms 80 per cent. of the available space within the stomach; the reticulum 5 per cent.; the omasum 7 to 8 per cent. and the abomasum the remainder.

Schalk and Amadon (*210*) have studied the motor functions of the bovine stomach by means of direct visual inspection, palpation and the gastric balloon. They made fistulous openings in the rumen 4 to 7 inches in diameter and of sufficient size to admit a man's hand and arm (Fig. 62). This portion of the stomach is in close approximation with the left abdominal wall and such an opening can be made at a point sufficiently high to avoid any great loss of fluid or solid ingesta (Fig. 63). Records
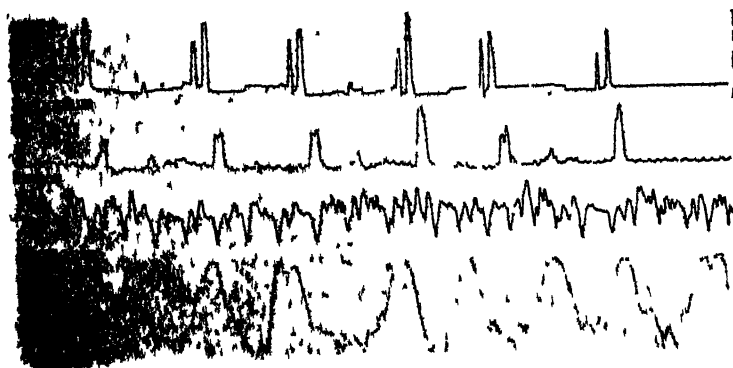
FIG. 64—Gastric activity in the different divisions of the bovine stomach. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

of the motility within all four divisions of the gastric complex have been recorded (Fig. 64).

According to these investigators the motility of the reticulum and rumen consists of a primary wave of peristalsis, originating in the region of the cardia and spreading progressively posteriorly, terminating in the ventral rumen structure. This is followed by a secondary peristaltic wave, originating about the anterior pillar and following the same course as the primary wave, and confining its activities entirely to the rumen. During rumination the motility is the slowest. At the cessation of rumination there is a perceptible increase in motility, which becomes markedly accelerated when the animal is eating. The phenomenon of regurgitation and the initiation of rumination are the culmination of a systematic succession of events governed probably by a complex reflex mechanism. With the

proper stimulus, moisture content, and volume of ingesta present, an extra-reticular contraction occurs just a fraction of a second previous to the regular reticular contractions. The cardia becomes submerged by a volume of porridge-like material, the glottis closes, the cardia opens funnel-like, the ingesta rush in, the cardia closes, and the bolus is formed and starts upon its retrograde course up the esophagus by antiperistalsis—aided possibly by a created vacuum.

It is further stated by these investigators that the center of sensitivity for the exciting of the reflex act of rumination is in the anterior dorsal region of the rumen in the vicinity of the cardia. The ingestion of food appears to diminish the amplitude of the omasal contraction and to increase their frequency. Rumination periods diminish the frequency of these contractions but improve the regularity of their occurrence. Lack of ingesta within the rumen stimulates the tonus of the muscular walls and the size of the cavity is greatly diminished, while in the empty state it exhibits almost constant movement.

HORSE

In the equine stomach it is interesting to note the small size of the organ as compared with the size of the animal, the capacity being between 3 and 4 gallons. The cardia and pylorus are in close proximity, the cardia being almost directly above the pylorus. The dorsal extremity of the organ forms an extensive blind pouch or *cul de sac,* termed the saccus cæcus, which extends eight to ten inches above the cardia.

Schalk and Amadon (*209*), in their preliminary studies on the gastric motility of this animal, used an ordinary toy balloon which was introduced via the naso-esophageal route and connected with a large water manometer (1 inch inside diameter). This animal is not suited for gastric fistula because of the distance of the stomach from the body walls. The use of the heavy walled balloon, and the uncertainty of getting the balloon into the same position in the stomach for the different periods of study, have probably led to considerable irregularity in the type of contractions recorded and to the registering of changes in tonus. It is evident, however, from the results reported, that hunger occurs in the equine stomach and even in the presence of relatively large quantities of food. The hunger state manifests itself in the form of more or less powerful contractions which may develop as early as five hours after feeding. These contractions appear in groups or periods separated by periods of relative quiescence, lasting from fifteen minutes to one hour or more in some animals (Fig. 65 [12 and 13]). The hunger contractions gradually increase in strength

FIG. 65.—12, gastric hunger contractions of the horse, sixty hours after feeding, showing sudden change from the active to the quiescent condition. 13, thirty-five minutes later, with the return of the periodic gastric hunger activity. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

until they finally end abruptly or in hunger tetany (Fig. 66 [14 and 15]). The periodicity and types of endings of the hunger activity periods are characteristic of those found in the stomach of man, monkey and dog,

FIG. 66.—14 and 15, gastric hunger contractions of the horse, ending in a prolonged period of incomplete tetanus practically identical with that of monkey and man. (Courtesy of Professor A. F. Schalk, The Ohio State University.)

with some variations in the duration of the active and rest periods. It is claimed further, although the results are not constant under all conditions, that the introduction of food into the stomach leads to the production of very rapid and powerful contractions which cease at the end of the feeding period, the stomach remaining in a period of almost absolute rest until it gradually comes out of this state and passes into regular digestive activity.

Dog (*Canis familiaris*)

It has been known for a long time that the young and growing individual experiences greater hunger than the adult or aged individual. This would appear to indicate that the hunger contractions of the stomach decrease with the age of the animal. If the gastric hunger mechanism is closely correlated with the animal's ˙actual need of food, one would naturally think that the activity of a young animal's stomach would be much more marked than that of an aged animal, for healthy young animals are usually more active than older ones and this indicates a greater metabolic activity on the part of the organism, to say nothing of the additional requirements for growth. Apart from this correlation of gastric hunger activity with the food requirements of the animals at different ages, it is probable that the gastric hunger mechanism itself "grows old," parallel with the aging of the animal as a whole, as is the case with most of the organs of the body. As a rule, the increasing age of an organ is paralleled by decreasing activity of the organ. The stomach of an old animal may therefore exhibit less vigorous hunger contractions because of the actual age of the stomach itself, irrespective of correlations with bodily needs.

Experiments were carried out on four groups of dogs of different ages, namely, on pups five weeks to six months of age, on young adults, on adults and on old adults (*165*). In all cases care was taken to select only dogs in good condition and perfect health, as far as could be judged by actions and external appearances. These dogs were operated on for gastric fistula according to the method described by Carlson (*44*) and as soon as the wound healed sufficiently, which usually required from five to seven days, the movements of the empty stomach were studied by introducing into the stomach a delicate rubber balloon which was connected with a chloroform manometer and used with a pressure of from three to six centimeters. The observations were made twenty-four hours after feeding, in order to assure an empty stomach. The animals were given at least one day or more of rest after each experiment so as to be in a per-

fectly normal condition when used again. During the taking of the records they were held in the lap, apparently without any appreciable discomfort, for they nearly always slept through a large part of the experiment. In fact, they became so well trained after a few trials that when removed from the cages they would follow the author from one room of the laboratory to another and watch for the first opportunity to jump into his lap in order to cuddle down and go to sleep. Five different series of records of the hunger movements of the empty stomach were obtained from each dog on five separate days, the continuous experimental periods ranging from two and one-half to four and one-half hours, respectively. This first series of dogs was then followed by a second similar series as controls.

In addition also to the two above series of dogs, a small pup five to six weeks of age was operated on for gastric fistula. This was on August 4,
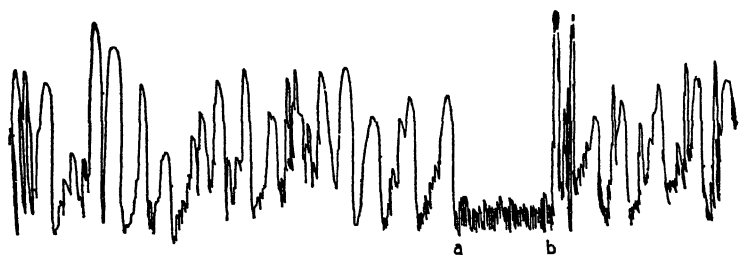
FIG. 67.—Tracings from the empty stomach of a very young pup, five to six weeks of age, showing the very rapid contractions and the very short quiescent period, a to b, of two and one-half minutes' duration. Water manometer. One-half the original size.

and three days later the wound had healed so that the first record of the stomach's movement was taken. Since this animal was so very small, it was necessary to use a smaller balloon and also a different manometer. The balloon used was of the same delicacy as those used on the older dogs, but was only about one-third as large. It was connected with a water manometer with three to six centimeters' pressure. As it was found impracticable to hold such a small animal in the lap, an office arm chair was selected and covered with a laboratory coat, the front of the chair seat being rather darkened and boxed in by raising the lower portion of the overlapping coat and attaching it. Here the pup was placed and after a trial or two he became so well accustomed to his new environment that nothing suited him better than a good long nap there. No control was run on this young pup because no other pup of that age was available, but of the series of records obtained several were of longer duration than any

TABLE X

Summary of observations on the length of the contraction and quiescent periods of the empty stomach of dogs of different ages.

	First Series of Dogs				Controls		
Dogs	Sex	Length of contraction period	Length of quiescent period		Sex	Length of contraction period	Length of quiescent period
Old adult	♀	30 min. to 2 hrs.	1 ⅙ to 3 ⅔ hrs.		♂	35 min. to 1 ¾ hrs.	1 ⅔ to 4 ⅙ hrs.
Adult	♀	1 ⅔ to 3 hrs.	1 ⅙ to 2 hrs.		♀	1 ½ to 3 hrs.	1 ½ to 2 hrs.
Young adult	♀	2 ¾ to 3 ¾ hrs.	1 to 1 ½ hrs.		♀	3 to 3 ¾ hrs.	1 ¼ to 1 ¾ hrs.
Pup (age 5-6 mos.)	♂	3 to 4 hrs.	5 to 10 min.		♀	3 to 4 ⅓ hrs.	5 to 10 min.
Young pup (age 5-6 wks.)	♂	4 ½ to 5 ⅔ hrs.	2.5 to 3.4 min.				
Prematurely born pups		Continuous	None				

taken on the other dogs, the longest one representing a continuous period of six and one-half hours, in which there was only one true rest period lasting two and one-half minutes (Fig. 67). This particular record was commenced eighteen hours after the feeding of the animal. All the records were taken on a slowly moving drum revolving at the rate of about fifty minutes per revolution. The time for the contraction and quiescent periods was figured by means of a chronometer record.

THE VARIATIONS IN THE HUNGER CONTRACTIONS OF THE EMPTY STOMACH
WITH AGE

The general character of the gastric hunger contractions in adult dogs has been reported by Carlson (*44*). After the introduction of the balloon into the stomach there is usually a short period of inhibition and as the dog becomes quiet there is an increase in the tonus of the stomach. The strong hunger contractions gradually increase in amplitude and the pause between them becomes shorter and shorter until the period usually ends in powerful and rapid contractions approaching incomplete tetanus. This is very evident in the older dogs and less so in the younger dogs, where the stronger contractions are going on practically all the time. Furthermore, the regularity of these movements is greatly disturbed and also inhibited for a longer or shorter period, depending on the disturbing influence, such as noise, fright, pain, anger, exciting influences, sight or smell of food, irritation—such as around the fistula due to the presence of gastric juice —or by an unhealthy condition of the dog. In all the dogs studied, the strong hunger contractions were usually preceded by restlessness as was shown by the twitching of certain skeletal muscles, slight groaning, or stretching and waking from sleep. At times these disturbances were noted in the upstroke of the curve, thus indicating that they are more or less disagreeable and painful to the animal. These effects appeared to be more magnified in the young animals than in the old, especially in the pups five to six weeks, and five to six months, of age, respectively.

The results summarized in Table X were computed from the tracings made from the different series of dogs and these figures in each case represent as nearly as possible the true time of activity and rest of the empty stomach, everything in the records of a doubtful character, or of an abnormal nature caused by disturbing influences, being entirely eliminated. A comparison of some of the records made from the different dogs may be had by a study of figures 67, 68 and 69. Carlson and Ginsburg (*51*) have extended the work of the writer to pups delivered by Caesarian sec-

FIG. 68.—Tracings from the empty stomach of an old dog, showing a complete contraction period, a to b, of thirty minutes' duration. Chloroform manometer. One-third the original size.
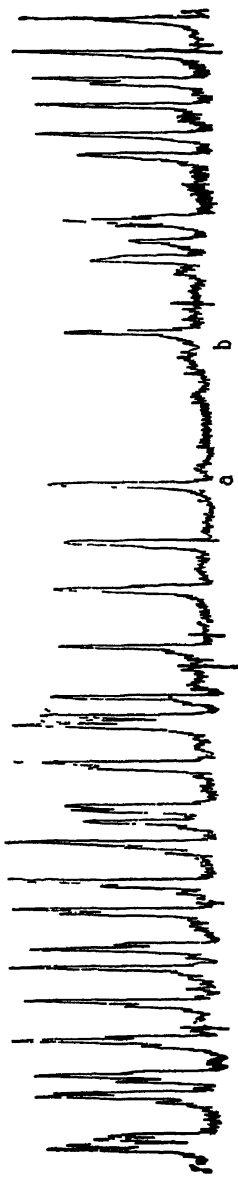
FIG. 69.—Tracing from the empty stomach of a pup, five to six months of age, showing the short quiescent period, a to b, of six and twenty-five hundredths minutes' duration. Chloroform manometer. One-third the original size.

tion eight to fourteen days before term, in which they found continuous motor activity of the empty stomach. In infants the typical hunger contractions begin from two and one-half to three hours after the previous nursing.

As regards variation of stomach movements between dogs of different ages, the chief and practically the only constant difference was found in the length of the periods of contraction and the periods of quiescence. In all cases the periods of quiescence are the longest in old dogs, varying from one and one-sixth to four and one-sixth hours, and rapidly decreasing in length, proportionate to age, of two and one-half to three and four-tenths minutes in the very young pup of five to six weeks. Conversely, the periods of contraction are the longest in the young dogs—for instance, in the very young pup the recorded periods run from four and one-half to five and two-thirds hours—and they rapidly decrease in length proportionate to age, in the old dogs from thirty minutes to two hours, thus showing that the stomach's activity is in direct proportion to the age of the animal.

The rapidity of the strong hunger contractions during the active periods appears on the whole to be greater in young animals than in old. The tonus of the stomach and also the strength of the contractions in young animals may be slightly higher, but they are subject to great variations. The decrease in the activity of the stomach as the animal approaches senility is probably an explanation, in part at least, for the more chronic gastric disturbances in the aged.

To summarize: in healthy dogs the hunger contractions of the empty stomach decrease with age. This decrease appears to some extent in the tonus and in the rapidity of the hunger contractions, but is particularly marked in the duration of the periods of hunger activity and the intervening periods of quiescence of the stomach. On the whole the decrease in the gastric hunger activity is proportional to the advance in age. In very young dogs the hunger contractions of the empty stomach are practically continuous.

Two factors are probably involved in this variation of the gastric hunger contractions; namely: (1) the actual age of the gastric motor mechanism; (2) the correlation of the gastric hunger mechanism with the metabolic gradient or the need of food. The relative importance of these two factors must be determined by direct experiment.

Further investigation (*166*) on prolonged fasting in young and old dogs has revealed the fact that in extreme stages of starvation there may be a prolonged Type III hunger contraction which also must be
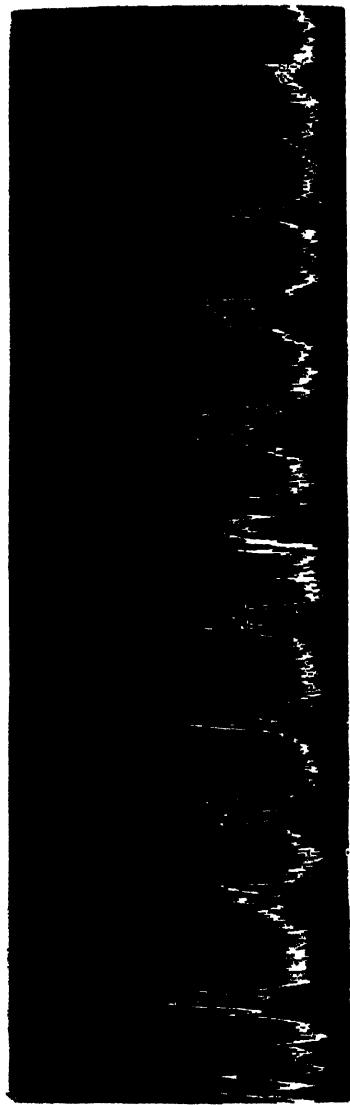
FIG. 70.—Type I. When stomach shows feeble tonus, the hunger contractions show an average duration of about 30 seconds, and the intervals between the contractions vary from half a minute to 3 or 4 minutes. This type of contraction usually falls into groups separated by intervals of relative quiescence. The duration of the groups varies from half an hour to three hours. The group usually begins with feeble contractions, which increase and then decrease; but rarely ever ends in tetanus.

FIG. 71.—Type II. When the stomach is in relatively strong tonus, the hunger contractions follow one another in rapid succession; that is, without any intervening pause. The duration of the contractions varies between 20 and 30 seconds. These contractions are frequently interrupted by periods of incomplete tetanus, lasting from 1 to 5 minutes, and the periods may last from 2 to 6 hours.
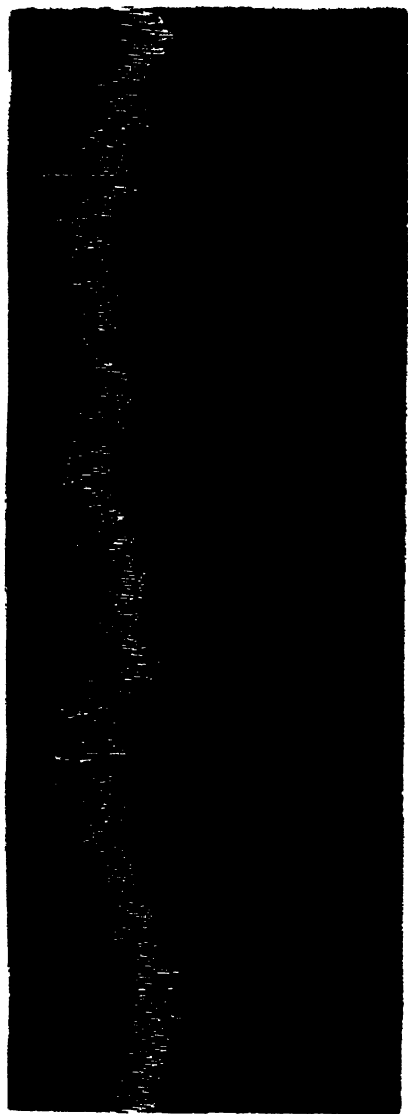
FIG. 72.—Type III. This type constitutes virtually an incomplete tetanus of the stomach. This tetanus is characterized by periods o strong and relatively persistent tonus on which are superimposed a series of rapid contractions. The duration of these rapid contractions averages 12 to 15 seconds, and the periods may last from 20 minutes to 2 hours.

dependent upon a certain degree of stomach tonus. This exaggerated type of hunger contractions appears to be of very short duration and is present only during the last 48 to 60 hours previous to the death of the animal from prolonged starvation, as indicated by my records. It always occurs in Type III hunger contractions (incomplete tetanus or strong stomach tonus) and consists of a very abrupt outbreak represented by an enormous increase in gastric tonus of the composition of incomplete tetanus which may even approach complete tetanus, superimposed upon the Type III contractions, which is then followed for a brief period after the relaxation from the extra tonus by hunger contractions characteristic
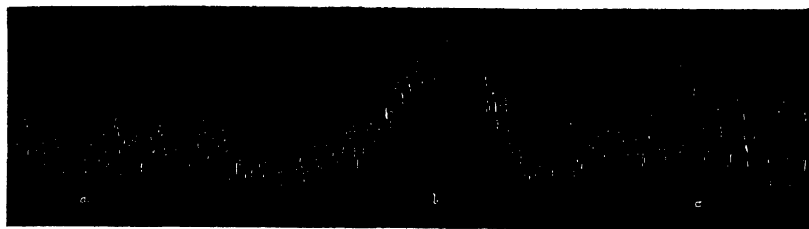
FIG. 73.—Tracing showing tonus and hunger contractions of young Dog B (Series I—control) after 360 hours (15 days) starvation; a, Type III contractions; b and c, prolonged Type III contractions showing strong tetany portion followed by characteristic Type II contractions on the tonus of Type III. Chloroform manometer. Black line below tracing = 0 mm. pressure. About two-fifths the natural size.

of Type II on the tonus of Type III contractions which gradually changes back into the true Type III contractions without any appreciable change in the gastric tonus. For the different types of hunger contractions in dogs see figures 70, 71 and 72. The length of the tetany periods of these prolonged Type III hunger contractions, as shown from the drum records, varies from about two and one-half to four minutes, and the duration of the entire period, including the tetanus and the characteristic Type II contractions, varies from about five to thirteen minutes. These periods gradually increase in length from their first appearance with the increase of the starvation until just a few hours before death when the gastric motor mechanism seems to lose its activity. A typical tracing illustrating this type of hunger contractions is reproduced in figure 73. In the following

brief protocols and elsewhere this exaggerated type of hunger contractions will be referred to as the prolonged Type III hunger contractions, the probable cause of which will be discussed more in detail later.

Series I. Dogs A and B. Control Experiments

Dog A (very old adult) :

July 20. Fast 29 hours. Type II hunger contractions feeble. Gastric tonus 3 cm. with increase to 4 cm. Slight tonus rhythm.

July 21. Fast 52 hours. Type II contractions. Gastric tonus 3 cm. with increase to 4.25 cm. Slight tonus rhythm.

July 22. Fast 76 hours. Type II contractions. Gastric tonus 3 cm. with increase to 4.25 cm. Slight tonus rhythm.

July 23. Fast 96 hours. Type III contractions. Gastric tonus 3 cm. with increase to 4.50 cm. Very slight tonus rhythm.

July 24. Fast 125 hours. Type III contractions (feeble). Gastric tonus 3 cm. with increase to 3.50 cm. Slight tonus rhythm. (Dog rather depressed. sore eyes, etc.).

July 25. Fast 148 hours. Complete absence of hunger contractions. Gastric tonus remains constant at 3 cm. No gastric tonus rhythm. (Dog ill with general dog distemper—heavy respiration).

July 26. Dog found dead in the morning.

Dog B (young pup 5 to 6 months) :

July 20. Fast 30 hours. Type II contractions. Gastric tonus 3 cm. with increase to 4 cm. Slight tonus rhythm.

July 21. Fast 53 hours. Type II contractions. Gastric tonus 3 cm. with increase to 4.50 cm. Slight tonus rhythm.

July 22. Fast 77 hours. Type II contractions (vigorous). Gastric tonus 3 cm. with increase to 4.75 cm. Slight tonus rhythm.

July 23. Fast 97 hours. Type II contractions. Gastric tonus 3 cm. with increase to 4.50 cm. Slight tonus rhythm.

July 24. Fast 131 hours. Type II and III contractions. Gastric tonus 3 cm. with increase to 4.75 cm. Slight tonus rhythm.

July 25. Fast 150 hours. Type II and III contractions. Gastric tonus 3 cm. with increase to 4.50 cm. Very slight tonus rhythm.

July 26. Fast 169 hours. Type II and III contractions. Gastric tonus 3 cm. with increase to 5.25 cm. Very slight tonus rhythm.

July 27. Fast 191 hours. Type II and III contractions. Gastric tonus 3 cm. with increase to 6.25 cm. Very slight tonus rhythm.

July 28. Fast 215 hours. Type III contractions. Gastric tonus 3 cm. with increase to 7 cm. Slight tonus rhythm.

July 29. Fast 239 hours. Type III contractions. Gastric tonus 3 cm. with increase to 6.50 cm. Very slight tonus rhythm.

July 30. Fast 263 hours. Type III contractions. Gastric tonus 3 cm. with increase to 6.50 cm. Slight tonus rhythm.

July 31. Fast 287 hours. Type III contractions. Gastric tonus 3 cm. with increase to 6.25 cm. Slight tonus rhythm.

August 1. Fast 317 hours. Type III and prolonged Type III contractions. Gastric tonus 3 cm. with increase to 6 cm. in Type III and to 7 cm. in tetany portion of prolonged Type III contractions, the characteristic Type II contractions keeping the same gastric tonus as Type III. Length of complete period prolonged Type III contractions 6 minutes; length of tetany portion 2.50 minutes. Slight tonus rhythm.

August 2. Fast 336 hours. Type III contractions. Gastric tonus 3 cm. with increase to 6.50 cm. Very slight tonus rhythm.

August 3. Fast 360 hours (15 days). Type III and prolonged Type III contractions. Gastric tonus 3 cm. with increase to 5 cm. in Type III and to 9.25 cm. in tetany portion of prolonged Type III contractions, the characteristic Type II contractions keeping the same gastric tonus as Type III. Length of complete period prolonged Type III contractions 13 minutes; length of tetany portion 4 minutes. Very slight tonus rhythm. (See Fig. 73).

August 3. Fast 368 hours (15⅓ days). Complete absence of hunger contractions. Gastric tonus remains constant at 3 cm. No gastric tonus rhythm, but a marked respiration. (At the time this record was taken the pup was in such a weakened condition from the long fast that the tracing was concluded after 30 minutes, when the animal passed into vomiting spasms.) The pup died in about one hour without the slightest struggle, apparent pain, or discomfort—simply worn out.

The protocols for Series II (Dogs C and D), Series I (Dogs A and B—first experiments), and Series III (Dogs E and F) are not given, since the same general characteristics are presented as in the preceding tabulations.

THE CAUSE OF THE VARIATIONS IN THE GASTRIC HUNGER CONTRACTIONS WITH AGE

The condition of the stomach's activity, if dependent alone upon the actual age of the gastric motor mechanism, ought to increase with starvation in old animals until it equalled that in the young animals, but since this is not the case, as is shown throughout the series of experiments, we must interpret the variations in the gastric hunger contractions as being produced not only through the factor of age but also through the rate of metabolism. This latter factor appears to be of the greater importance in determining the activity of the gastric motor mechanism. Therefore, this retarded activity, as seen in the gastric hunger contractions of old animals, must be due to a slower rate of metabolism brought about and controlled chiefly through the age factor. There was a slight increase in the amplitudes of the hunger contractions during the first few days of starvation followed by a gradual decline. This slight in-

crease occurred in all the dogs with but one exception, namely, in the old dog of Series I, the first experiments in which the hunger contractions were feeble. This particular animal was very old and the person from whom she was obtained claimed that she was over eleven years of age. This statement was probably authentic, since her general appearance and loss of teeth indicated it. The old dogs of the other two series were younger (probably not over seven or eight years of age), and the hunger contractions were vigorous and did not show this feeble type.

The feeble contractions in this very old dog are probably identical with the contractions in those animals with which Boldyreff (17) worked, for like his, the hunger contractions were feeble during the first few days (first experiment, Series I—Dog A), then there was a slight increase in the amplitude followed by the usual and gradual decline. This increase in the strength of the hunger contractions after the first few days of starvation does not corroborate entirely the results of Boldyreff, since he states that after the first three or four days there is a copious and continuous secretion of gastric juice, which, of course, will lead to the inhibition of the hunger contractions if the normal percentage of HCl is present (42, 43). The small and feeble contractions during the first few days may possibly be explained by supposing that there is a hypersecretion of the gastric juice sufficient to produce a partial inhibition of the hunger contractions, for there seems to be no question but that there is a secretion of gastric juice in this animal during the first few days at least, judging from the quantity of fluid that escaped through the fistula; and besides, the animal appeared perfectly normal. Later there is the increase in the strength of the contractions, which may also be explained by assuming that the amount of NaCl in the blood, the principle source of the HCl of the gastric juice, is greatly diminished by the complete elimination of the animal's food, the only source of NaCl left being the very small quantity found in the water to which the animals always had free access. Thus, if the percentage of HCl is reduced in the gastric juice after the first few days, the partial inhibition produced by it is also practically removed and we would expect that the above increase in the strength of the hunger contractions, which is of only a brief duration, would then be followed by the characteristic and gradual decline.

A comparative study was made of the amplitudes of the hunger contractions in the old and young animals. In both the old and young dogs there appears to be an increase in the amplitudes of the hunger contractions during the first few days of starvation, followed by a gradual decline which continues to the death of the animal with the exception of a por-

tion of the prolonged Type III contractions which appear only in the extreme stages of starvation. At no time do the amplitudes of the hunger contractions for the old dogs equal those of the younger ones, except in one case (Series III—Dogs E and F), where both the old and younger dogs were continued through a period of prolonged starvation until one of the animals died. Here, on the ninth day of starvation, the amplitudes of the old dog's contractions surpassed those of the pup, thus showing only the greater endurance of the older animal. In Series III—Dog E, on the third day of starvation there was a decided fall in the amplitude of the old dog's contractions, but this was probably the result of some disturbing influence, or perhaps to a slight depression in the animal, since it rose on the fourth and was continued on the fifth day to a degree which

Fig. 74.—Tracing showing the hunger contractions of old Dog E (Series III) after 144 hours (6 days) starvation with a marked increase in the gastric tonus. Chloroform manometer. Black line below tracing = 0 mm. pressure. About two-fifths the natural size.

corresponded well with the second day's record (Fig. 74). In Series I—control—Dog A, too much stress should not be laid on the old dog's contractions, since she became ill on the fifth day with nose and eye infections which developed into a general pulmonary infection. She died two days later. However, this did not seem to change materially the original results, as shown by the first experiments on this animal, except that the amplitudes of the hunger contractions dropped more rapidly and somewhat lower after the animal became ill. The tonus was also as markedly affected, as is shown by the protocols. This is an excellent example of the inhibition of the hunger contractions through depression.

The protocols show that there is a marked increase in the gastric tonus during starvation up to within a few hours of the death of the animal and

this increase in the gastric tonus appears to be directly proportional to the decrease in the amplitudes of the hunger contractions (Fig. 75). It appears also that some dogs may exhibit a strong stomach tonus at the beginning as in Series III—Dog E, while others may show relatively low tonus as in Series I—Dog B, and these are subject to only slight variations as shown by the controls, but in all cases, the tendency is a gradual
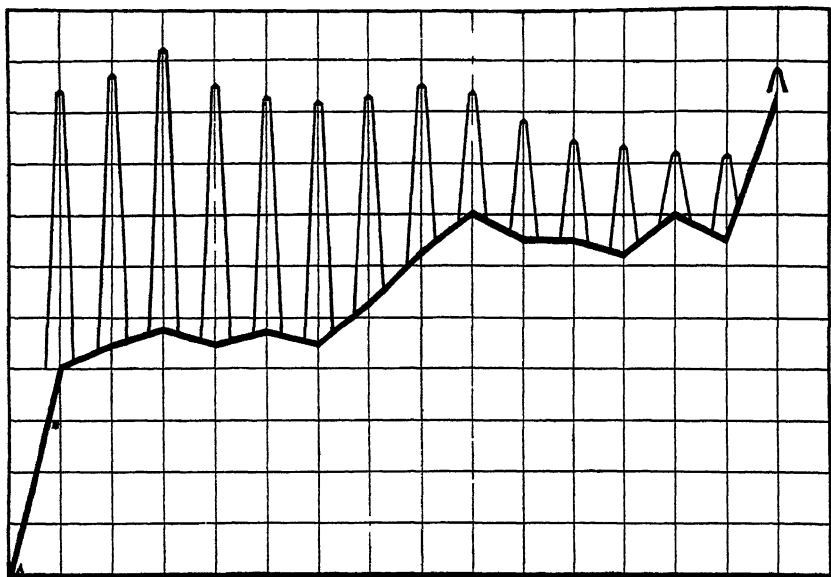
FIG. 75.—Diagrammatic representation of the lowered amplitude of contraction on the base of the rising tonus as constructed from the daily tracings of young Dog B (Series I—control). Each of the above squares represent one sq. cm. The erect pyramids indicate the amplitudes of the hunger contractions in centimeters arranged on the rising tonus as a base line. Spaces left to right indicate number of days of starvation; spaces bottom to top daily increase in the gastric tonus in centimeters. Heavy line at bottom of chart = 0 mm. pressure of chloroform manometer. A to B = constant pressure of 3 cm. used throughout the experimentation. Note the rapid increase in gastric tonus and decline in amplitude of contractions on the fifteenth day as produced by the prolonged Type III hunger contractions.

increase in the gastric tonus irrespective as to whether the animal starts off on a high or low gastric tonus. As has been stated before, the different types of hunger contractions are dependent upon a particular degree of stomach tonus, and this increase in the tonus during starvation is accompanied by a progressiveness in the type of hunger contractions; that is, by an advance from the lower to the higher types, respectively. To illustrate: If an animal's stomach starts off with Type II hunger contractions, the tendency is a progression first to Type III contractions and then to

prolonged Type III contractions. If it starts off with Type I contractions the progression is through the different types of hunger contractions from I to III inclusive. However, some dogs (Series III—Dog F) may show during the first few days of starvation an alternation between the Type I and II contractions, but the final result is always the same, namely, a progression from the lower to the higher types of hunger contractions. Therefore, the increase in the gastric tonus appears also to be directly proportional to the advance from the lower to the higher types of hunger contractions.

Prolonged starvation leads to increased activity of the gastric motor mechanism as indicated by the rise in tonus, at least, until that point is reached where the stomach becomes involved in the general debility and cachexia. Since the animals were allowed only water the energy necessary for their continued existence must have been met by the destruction of such stored up materials present in their own bodies as circulating and tissue protein, fat and glycogen. The last substance is quickly used up since it is present only in comparatively small quantities, and so the animal becomes emaciated since it lives upon its own body protein and fat. We know that the stored up body fats, by a reversible lipolytic reaction, may be converted over into soluble fats and oxidized by the cells to give heat and energy to the body. There is also evidence of "circulating protein" in starvation as food for the tissues. Thus, Miescher (*146*) showed that the salmon virtually starves, after entering the Rhine from the sea, whereas the genital organs of both the male and female greatly develop. This he claims is at the expense of the muscle tissue which, to use the author's exact figures, may lose as much as 54.74 per cent. of their weight. Voit, in his work on starving animals, also believes in a "circulating protein," and that the "organized protein" of the tissues themselves is gradually changed over in some way to the "circulating protein" and transported by the blood to the tissues needing nourishment. Luckhardt and Carlson (*124*) have reported on the possibility of a "hunger hormone" which gradually accumulates from the body tissues—in general, probably before the tissues actually demand additional fuel (food)—which is transported by the blood to the gastric motor mechanism and there stimulates that organ to activity, hunger contractions. A gastric tonus rhythm is also evident which seems to be present in nearly the whole series of experiments (Fig. 76). This tonus rhythm is probably produced by a reflex excitation through the motor nerve fibers which play upon the oxidative processes in the tissues, thus augmenting at one time and inhibiting at another the physiological oxidations.

LOSS OF HUNGER SENSATION WITH PERSISTENCE OF HUNGER CONTRACTIONS

Many cases of prolonged starvation in men and women have been cited by Carrington (56), where the hunger sensation subsided or disappeared after the third day. Viterbi, who voluntarily starved himself to death, noted complete absence of hunger after the fifth day (122), and the depression of this hunger sensation seems to be confirmed by the work of Carlson (46) on men and dogs. In dogs under observation it was noted that after the first four or five days of starvation there was a depression of the hunger sensation, although the gastric hunger contractions persisted. This is explained by supposing that the neurones in the central nervous system, which have to do with the sensation of hunger, become fatigued after the first few days, thus eliminating entirely the hunger sensation, although the gastric hunger contractions are evident. In addition to this loss of the hunger sensation, the return of the strong hunger contrac-

FIG. 76.—Tracing showing the hunger contractions of old Dog A (Series I) after 121 hours (5 days) starvation with a marked gastric tonus rhythm. Chloroform manometer. Black line below tracing = 0 mm. pressure. About two-fifths the natural size.

tions as the prolonged Type III contractions must be considered, and the following considerations might be offered not only as a possible but also as a probable explanation. These characteristic hunger contractions which appear only in the extreme stages of starvation after the gastric motor mechanism has become hypersensitive from the long continued starvation must be due, either to a heat CO_2 stimulation from the protein of the circulation, or to an anemic stimulation of the stomach owing to the moribund state of the circulation, since the gastro-neuro-muscular apparatus has become entirely independent of the central nervous system. A typical tracing showing this supposed stimulating action of asphyxia or anemia on the hunger mechanism is reproduced in figure 73. Rogers (200), in his work on rabbits, has spoken of prolonged contractions or periods of tetany lasting from two to three minutes in the last stages of

starvation. These are probably identical with the prolonged Type III hunger contractions in dogs.

The variations in the gastric hunger contractions are dependent upon two factors, namely: the actual age of the stomach tissue itself and the diminished rate of metabolism in the animal's entire body, which may imply a smaller quantity of chemical stimuli to the gastric hunger mechanism in the circulation. The latter seems to be of the greater importance in determining the activity of the gastric motor mechanism. Although starvation causes some increase in the vigor of the stomach tonus and contractions in the old dogs, it is not, however, the prime factor. Since the actual age of the gastric tissues is the most important element, we cannot offer further explanation until we know what constitutes the physiological aging of the tissues.

The increase in gastric tonus during prolonged starvation is directly proportional to the advance from Type I to Type III hunger contractions, and inversely proportional to the decrease in the amplitudes of the hunger contractions.

Other important gastric references on the dog concerned with this investigation have been made elsewhere in this paper.

MONKEY (*Macacus irus, Macacus rhesus* and *Cynocephalus anubis*)

Since the celebrated experiments of Beaumont (*12*) on the stomach of Alexis St. Martin, nearly a century of experimentation in gastric physiology has not solved completely the problem of the inner controlling factors concerned with the movements and tonus of this organ. Many factors which might influence the process, as nervous, chemical or "hormone," pressure and temperature, have been investigated, but it has always been a question how nearly the conditions approach those of normal activity. In higher animals the movements of the empty stomach (hunger peristalsis) are periodic in character and more vigorous than the peristaltic movements of digestion which normally commence a few minutes after the entrance of food into the stomach and continue until all the nutrient material in the form of chyme has been passed on into the small intestine.

The character of the periodic and motor activity of the empty stomach in man has been reported (*40*). Since the motor activity in the stomach of the dog (*44, 166, 167*) exhibits certain variations from that of the human, the monkey was selected for this experimental investigation because of the ancestral relationship which it is assumed to bear to man in the evolutionary process of animal development. This so-called rela-

tionship would be suggestive of the closest parallelism existing between the gastric activities of these two Primates. Furthermore, Carlson has shown that in the dog (*44*) and in man (*42*) the movements of the empty stomach may be modified by psychic stimuli, though only in the direction of inhibition, and that in the dog they continue even when the stomach has been isolated from the central nervous system by section of the vagi and splanchnic nerves. After such section, inhibition of tonus and contractions may still be obtained by stimulation of the gastric mucosa through local automatism or reflex action, but it is diminished both in intensity and duration. Cutting the vagi leaves the stomach in a permanently hypotonic condition (*44*). It is evident that the central nervous system acts merely as one of the regulators of this reflex mechanism but for how much of the regulation the cerebrum is responsible and what part is played by the mid-brain and medulla is still open for further investigation. On the other hand, Alvarez (*4*) has attempted to explain most, if not all, the motor phenomena of the gastro-intestinal tract on the basis of a purely muscular gradient of rhythmicity, denying local reflexes in the intestine itself, and minimizing the importance of the extrinsic nerves in the control of the gastro-intestinal tract. Therefore, it is the purpose of this communication to present in some detail data which confirm and extend the findings on gastric behavior in man.

In view of the fact that the literature on the nature of the sensation of hunger is exhaustively reviewed in Carlson's book (*47*), the reader is referred to that source for a further general consideration of the problem.

<center>ANIMAL MATERIAL</center>

The experiments forming the basis of this report were made by Patterson, Illenden, Rubright and Scott (*182*) on Javanese and Ringtail monkeys (*Macacus irus*[3] and *Macacus rhesus*) and one baboon (*Cynocephalus anubis*). Forty-nine healthy young animals were used. The Javanese monkeys were obtained from an animal importer at San Francisco and the others from importers in New York.

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[3] A communication from Tracy I. Storer, Inspector of Foreign Birds and Mammals, Port of San Francisco, U. S. Department of Agriculture, Bureau of Biological Survey, reads as follows.—"Your request for information on the Javanese Monkey is not an easy one to answer. There is a great deal of doubt in the minds of people who have worked on the monkeys of that group as to just what name should be applied. I think that the name *Macacus irus* or *Pithecus irus* is the one commonly applied to this form. In any event, the use of this name will be as nearly correct as any which you can use."
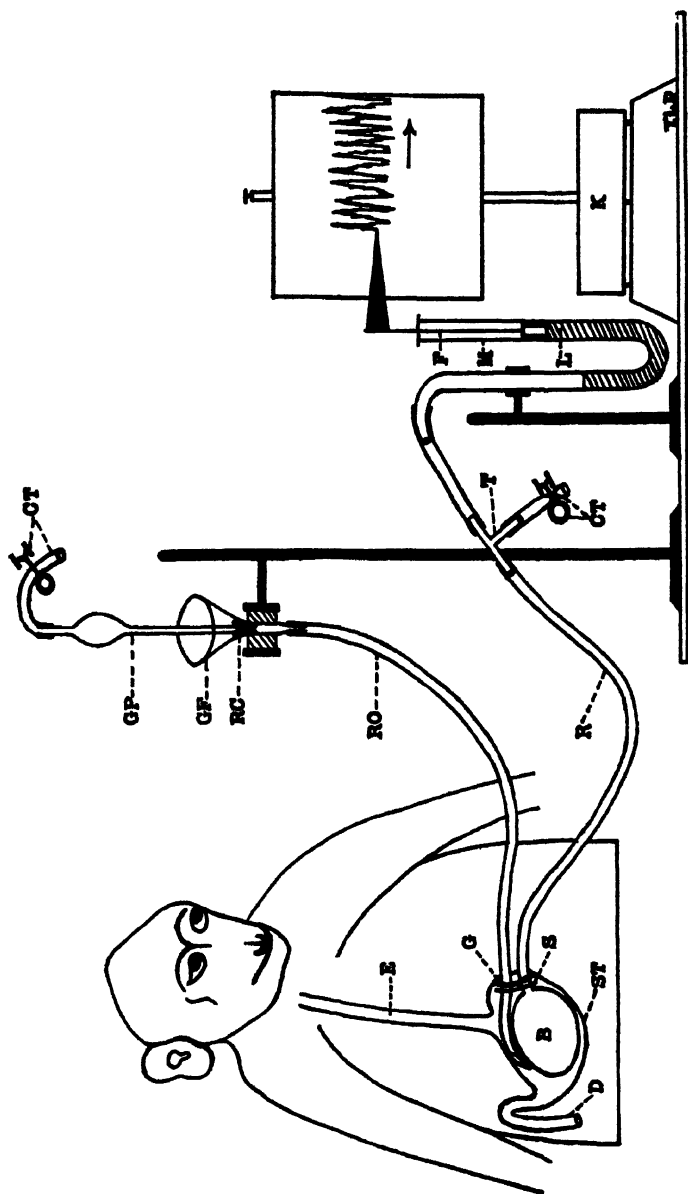
FIG. 77.—Diagram showing method of recording gastric motility and the effect of inhibitory substances on the monkey's stomach. K, kymograph; F, glass float with recording flag; M, manometer; L, manometer liquid (water); T, glass T-tube for inflation of balloon; R, rubber tube connecting balloon with manometer; G, gastric fistula (gastrostomy) in the fundic end of the stomach; B, balloon in stomach; E, esophagus; ST, stomach; D, duodenum; CT, clamp and rubber tube; GP, glass pipette for introducing liquid substances directly into the stomach; GF, glass funnel; RC, rubber cuff on end of pipette; RO, rubber tube with open end in stomach; S, silk thread holding rubber tubes together in the stomach.

Fig 78 — Monkey III   Susie   Riding on the shoulder of an assistant   Note the friendliness and contentment

The Javanese monkeys were employed chiefly in the earlier experiments in a study of the movements of the empty stomach   Although so-called tamed monkeys were purchased, none was sufficiently trained for the particular type of experimentation in question   In fact, unlimited patience was required during the many weeks of preliminary training and even then it was found impossible to tame some of the animals, after employing every conceivable means.

EXPERIMENTS ON NORMAL ANIMALS

The animals trained to permit handling were operated on and provided with gastric fistulæ in the fundus of the stomach, after the method of Carlson (44) on dogs In from five to seven days the wound was sufficiently healed to permit the recording of the gastric hunger contractions by the balloon method with the animal lying quietly in the lap of an attendant (Fig 77).

Fig 79 —Monkey III Susie   Asleep in the arm of an assistant   Note the complete relaxation

Since monkeys are so deeply concerned in what goes on around them, it was necessary either to partition off a corner of the laboratory for the animal and the attendant or place them in an adjoining room with the rubber tubes and electric signaling wires passing through the wall. The activities of the kymograph operator occupy the attention of the animal to such an extent as to interfere with the normal gastric activity. So observant are the animals that even the crawling of a fly on the wall or ceiling will attract sufficient attention to lead to restlessness and interference of the normal movements of the stomach. A darkened room is preferable and, when an attendant knows how to handle a trained monkey, even a hungry one will lie quietly for three or four hours and will usually cuddle up and sleep for a considerable portion of the period.

Eight animals were used in this study of the normal movements of the empty stomach, three of them trained to a point of proficiency, thus permitting the recording of the normal gastric activity. One of them, "Susie," became a real pet and was given the freedom of the laboratory. There was nothing she enjoyed more than to ride on our shoulders, (T. L. P. and J. I.), even clinging to maintain her balance while we were busily engaged in other duties. In the quietness of the laboratory she was perfectly at ease and apparently happy (Figs. 78, 79 and 80).

Studies were made on the movements of the empty stomach 18 to 24 hours after feeding, and graphically recorded on a sixty minute drum. A water manometer was used, with a pressure of from three to six centimeters, and the animals were given a rest period of at least twenty-four hours following each experimental observation, in order to keep them in normal physiological condition.

ACUTE EXPERIMENTS

In the earlier phases of this work considerable fluctuations in gastric tone and reflex inhibition were observed. As a result, a series of acute experiments were inaugurated in an attempt to determine the effects of nerve influence on the tonus and motor activity of the gastric mechanism. All these later experiments were performed under light ether anesthesia in order to preserve the reflexes. The esophagus, vagi and carotids were exposed in the neck. A lateral incision through the wall of the esophagus admitted the stomach balloon for the recording of the gastric movements. The blood pressure was recorded simultaneously from the carotid or femoral artery and the splanchnic nerves were isolated laterally at the edge of the deep muscles of the back, for stimulation. In these acute

experiments a fast of from forty to forty-eight hours was found to be more satisfactory.

THE CHARACTER OF THE MOVEMENTS OF THE EMPTY STOMACH OF THE MONKEY

The movements of the empty stomach in mammals were first studied by Boldyreff (*17, 18*) in dogs by means of the gastric fistula. Rubber balloons were introduced into the stomach and connected by air or water transmission to the recording manometer for graphic registration. Ac-

FIG. 80.—Monkey III, "Susie." Showing characteristic position taken by animal during graphic registration of the movements of the empty stomach. Gastric fistula not shown in picture.

cording to this investigator the empty stomach of the dog exhibits alternating periods of rhythmical contractions and periods of complete quiescence during the first three or four days of fasting. The periods of activity vary in length from twenty to thirty minutes and the intervening periods of rest last from one and one-half to two and one-half hours. The period of activity begins with weak contractions and these increase gradually in strength until the period ends abruptly with the strongest contractions.

Cannon and Washburn (*39*) have reported similar results from the empty stomach of man by introducing a balloon through the esophagus into the stomach. The observations were made six to twenty hours after meals and were directed towards establishing the relation between the contraction periods of the stomach and the sensation of hunger. They seem to agree with the previous investigator in the absolute quiescence of the stomach between the periods of the strong rhythmical contractions.

Our knowledge of gastric physiology has also been greatly advanced by the work of Carlson (*40, 41, 42, 43, 44, 45, 46, 47*) in an extensive series of studies carried out, not only on animals, but on a young man in normal health with a permanent gastric fistula—Fred Vlcek, the so-called second Alexis St. Martin. By the use of more delicate methods, Carlson (*46*) has analyzed the various types of motor activities of the empty stomach during prolonged fasting, in which he has described three types.

<div align="center">TYPES OF HUNGER CONTRACTIONS</div>

1. Rhythmical contractions of about twenty-seconds duration and designated the "twenty-seconds rhythm."

2. Very vigorous contractions occurring periodically, of about thirty-seconds duration and designated the "thirty-seconds rhythm."

3. Tonus changes of the stomach musculature.

While there is some indication of a feeble tonal rhythm during the rest period in one of the published tracings (Fig. 2) of Cannon and Washburn, the methods used by these investigators and more particularly by Boldyreff (*17, 18*) were not delicate enough to record the weaker contractions and the variations in tonus.

In dogs the movements of the empty stomach, as registered by means of a delicate balloon in the fundus, have been classified by Carlson (*44*) into three distinct types, namely, Types I, II and III, each of which is thought to be dependent upon a particular degree of stomach tonus (Figs. 70, 71 and 72). Type I is exhibited when the stomach shows feeble tonus and the contractions have an average duration of about thirty

seconds with the intervals between the contractions varying from half a minute to three or four minutes. Type II is exhibited when the stomach is in relatively strong tonus, the contractions following one another in rapid succession; that is, without any intervening pause. The duration of the contractions varies between twenty and thirty seconds. These contractions usually occur only in young and vigorous individuals in excellent physical condition. Type III is exhibited when the stomach constitutes virtually an incomplete tetanus characterized by periods of strong and relatively persistent tonus on which are superimposed a series of rapid contractions. The duration of these rapid contractions averages from twelve to fifteen seconds and they are thought to be analogous to the twenty-seconds rhythm in man.

The three types of contractions may be observed in the same dog on different days, or Type I may be exhibited for a few days and then be superseded by Type II, etc. In general, Type I predominates in some dogs and Types II and III in others, while some of the tracings exhibit transition stages. This is to be expected, since the types of hunger contractions seem to vary with the degree of gastric tonus, and this tonus may vary considerably during a single observation period. In man, however, the movements of the empty stomach are confined more especially to the twenty and thirty-seconds rhythms and, although similar in character, they do not correspond in every detail to the three types of gastric hunger contractions exhibited in the dog's stomach.

The contractions of the empty stomach of the monkey, as registered by means of a delicate rubber balloon in the fundus, are practically identical with those of man. The stomach of this animal exhibits a definite periodicity, characteristic of the gastric hunger activity of higher animals, the contractions falling into groups, separated by intervals of relative quiescence. The duration of the groups or periods of hunger activity vary from one hour and forty minutes to two hours; the quiescent or rest periods, from ten to twenty minutes, thus making the monkey occupy a somewhat intermediate position between the five to six months' old pup and the young adult dog. The rest periods appear to be short but, as previously stated, only young, vigorous animals were employed in these experiments in which the gastric activity is thought to be dependent upon the factor of age. This is to be expected, since the author (*165*) showed conclusively in the case of dogs of different ages that the periods of quiescence are the longest in old dogs. These periods range from one and one-sixth to four and one-sixth hours, and rapidly decrease in length proportionately to age, being from three and four-tenths to two and one-

half minutes in the baby pup of five or six weeks. Conversely, the periods of contraction are the longest in the baby pup. These periods range from four and one-half to five and two-thirds hours and then rapidly decrease in length proportionately to age in the old dogs from two hours to thirty minutes, thus showing that the stomach's activity is in direct proportion to the age of the animal.

These results on the rhythmical contractions of the empty stomach in dogs are not in accord with those of Boldyreff (17), since his account of this rhythm is incomplete and partly misleading. The length of both the contraction and the quiescent periods as observed by Boldyreff seems, on the whole, to be considerably less than that shown in the author's series of old dogs (165), and they are also practically identical with those reported by Carlson (44) on adult dogs. According to Boldyreff (17) the contractions always come in groups of from twenty to thirty minutes duration, and during the one and one-half to two and one-half hours interval between these groups the stomach is completely quiescent. The contractions observed were probably those of a feeble Type I group, but it is evident this investigator never obtained the Types II and III rhythm in his animals.

The difference in the results of Boldyreff (17) and those of Carlson (44) and the author (165) is probably due to the condition of the animals, the method of handling, and the method of registering the stomach contractions, for Boldyreff's dogs were forced by mechanical means to lie or stand in one position for six to twelve hours at a time. This forced position, as well as the classical silver cannula used in the gastric fistula, probably in part produced the brevity of the contraction periods, for all such influences tend to depress the gastric activity. Furthermore, all of these dogs, in addition to the gastric fistula in the fundus of the stomach, also possessed duodenal, pyloric, pancreatic or hepatic fistulæ. The animals, therefore, were subjected to much greater disturbances of digestion and metabolism than the animals under discussion in this paper, which were permitted to lie comfortably in the lap of an attendant and usually without restraint, a condition which is certainly more nearly normal. In addition, Boldyreff's published tracings do not show the respiratory intragastric pressures, nor do they indicate the slightest variations of the gastric tonus during the observation periods. It is, therefore, evident that his recording apparatus was not delicate enough to detect small variations in the intragastric pressure.

In man and dog the fundic end of the stomach, during normal digestion, exhibits a slow tonus rhythm which, during the emptying of the

stomach and the onset of the hunger period, becomes more vigorous (*204*). Upon this slow rising tonus rhythm the peristaltic waves arise from points higher and higher toward the cardiac end of the stomach and sweep downward over the organ.   In all observations on the monkey the empty stomach exhibits, on the whole, greater tonus and motor activity than the filled
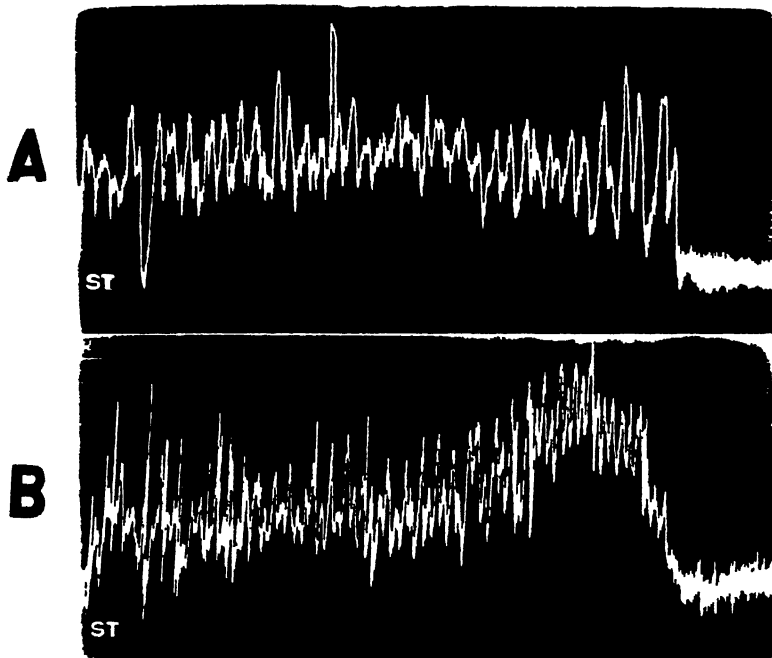

Fig. 81 —Monkey III, "Susie." Records of the contractions of the empty stomach of the normal young adult. A, final twenty minutes of a typical period of hunger contractions twenty-two hours after eating. B, final twenty minutes of a typical hunger period after a fast of twenty-seven and one-half hours. Note in tracing B the prolonged period of incomplete tetanus at the culmination of the hunger period, and the reappearance of a feeble 20-second rhythm immediately following the cessation of the period of strong hunger contractions. Note also the increase in the tonus and the hunger contractions of the empty stomach during prolonged fasting. Water manometer. St, Stomach contractions. About one-half the original size.

stomach.   In this animal two types of rhythmical contractions have been observed, which alternate with periods of relative quiescence.   The individual contractions of the more powerful type have a duration of about thirty seconds and are comparable to the "thirty-seconds rhythm" in man.   The other pressure rhythm, thought to be due to a tonus contraction of the fundus or peristalsis of the antrum, has an individual dura-

tion of approximately twenty seconds and is likewise comparable to the "twenty-seconds rhythm" in man.

No feeble contraction periods have been observed in any of the monkeys studied, due, evidently, to the fact that all the animals were young and vigorous.   Such contractions would more likely occur in old animals or those in a state of depression from illness or other disturbing factors. The contractions forming the periods of strong hunger activity usually begin as feeble tonus rhythms, which gradually increase in amplitude with a simultaneous shortening of the intervening intervals of rest, and may or may not end in tetanus or prolonged tonus contractions, followed by a relatively abrupt relaxation and quiescence in which only a respiratory pressure rhythm is present (Fig. 81 A).   The periods of more powerful contractions are also initiated by weak contractions with rather long intervening pauses, which gradually become shorter as the amplitude of the individual contractions increase, until the climax is reached in a number of very powerful and rapid contractions of the order of incomplete tetanus.   The tetanus usually lasts from two to five minutes and the cessation of these periods of hunger activity is always abrupt (Fig. 81 B). This prolonged period of incomplete tetanus at the culmination of the hunger period, with the reappearance of a feeble twenty-seconds rhythm immediately following the cessation of the period of strong hunger contractions, is frequently seen in the monkey's stomach and corresponds to that observed by Carlson (46) in man.   It more often occurs in prolonged fasting or in cases where there is a considerable increase in tonus and the hunger contractions of the empty stomach.

These results seem to challenge the correctness of the statements of Boldyreff (17) and of Cannon and Washburn (39) that the stomach is completely at rest between the periods of the thirty-seconds rhythm. Mangold (130) also claims that the completely empty muscular stomach of the buzzard is quiescent, but Rossi (205) maintains that the activity of the stomach of chickens is more vigorous when empty than during digestion.   In the monkey there is an increase in the gastric tonus and the hunger contractions and the intensity of this activity is also evidenced in the appearance of the incomplete hunger tetanus.   The gastric hunger contractions in monkeys also go on in sleep with the same frequency and intensity as during the waking state, as has been determined by continuous gastric registration covering periods of from four to six hours in which the animals have slept during portions of these periods.

During the quiescent periods of the stomach the animals are more at ease and more likely to drop off to sleep than is the case during the strong

periods of hunger activity. The strong contractions arouse and may even awaken the animals from sleep and they sometimes moan. As a result, they become restless, because of the discomfort of the hunger pangs, which are primarily produced by the contractions of the wall of the stomach.

THE INHIBITION OF THE MOVEMENTS OF THE EMPTY STOMACH OF THE MONKEY

Inhibition by Acid and Alkali

The tonus and hunger contractions of the empty stomach in man and dog are temporarily inhibited by mechanical and chemical stimulation of the nerve endings in the mucous membrance of the mouth, the esophagus, and the gastric mucosa (*43, 45*). Brunemeier and Carlson (*26*) have, however, produced similar inhibitory action on the dog's stomach from stimulation of the intestinal mucosa. The stomachs of many other animals also respond in an inhibitory manner, as is shown in rabbits, pigeons, frogs and molluscs (*200, 201, 177, 168, 170*). Gastric inhibition in the monkey is practically identical with that in man and the higher animals.

When water, 1 per cent. sodium carbonate, or 0.5 per cent. hydrochloric acid, are introduced slowly and directly into the stomach through a pipette and small rubber tube passing through the gastrostomy opening, they invariably produce inhibition, the degree of intensity of the inhibition being increased by the substances as listed in the order of their potency (Fig. 77). The duration of the inhibition depends upon the quantity and nature of the material introduced and varies in its degree with the stimulating power of the substance employed. Water, although the least effective of the three substances used, produces a marked fall in gastric tonus with a temporary inhibition of the hunger contractions of from two to three minutes duration (Fig. 82 A). The water introduced into the stomach was at room temperature and apparently produced the inhibition through a stimulation of the nerve endings in the gastric mucosa, either by mechanical pressure or by osmosis. According to this view, the passage of the water out of the stomach into the intestine, or the addition of sufficient salts to prevent stimulation by hypotonicity, would mark the cessation of the inhibition. The water (10 cubic centimeters) was probably not cold enough or in sufficient quantity to stimulate the protopathic temperature nerve endings in addition to those acted upon by pressure and osmosis, so that the results overbalance any error that might be ac-

counted for by the cold water cooling the air in the balloon and thereby temporarily lowering the tension to an appreciable degree.

The introduction of 10 cubic centimeters of sodium carbonate, 1 per cent. solution, directly into the monkey's stomach, produces a more pronounced inhibitory effect than water. This inhibition is probably the result of the alkalinity rather than of the bulk of the solution, since Carlson (43) has shown that in the stomach of man sodium carbonate in concentrations of 0.2 per cent. or less appears to have the same influence on the hunger contractions as equal quantities of water. In greater concentration (0.2 to 1.0 per cent.) the degree of inhibition produced is on the whole directly proportional to the concentration and the quantity of
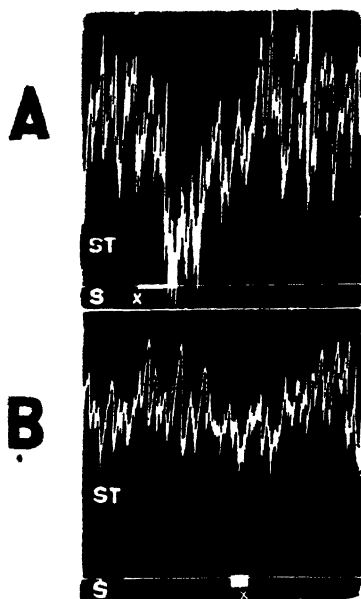

FIG. 82.—Monkey III, "Susie." Records from the empty stomach of the young adult. A, part of a period of strong hunger contractions twenty-two hours after eating. At x, 10 cc. of water introduced directly into the stomach, producing a temporary inhibition with a lowering of the gastric tonus. B, hunger contractions after a fast of twenty-five hours. At x, the pad of the hind foot was tickled while the animal was asleep. Note diminution in amplitude of contractions. Water manometer. St, stomach contractions. S, signal. About one-half the original size.

the solution introduced into the stomach. For example, an introduction of 5 cc. of sodium carbonate into the monkey's stomach may or may not produce the temporary inhibition. Alkalinity produces the same effect on the stomach as acidity, only to a lesser degree, both acids and alkalies causing inhibition without any after effect·of the nature of augmentation. Since sodium carbonate in a 0.2 per cent. solution or less has no more effect on the hunger motility than equal quantities of water, it would seem to indicate that a slight alkalinity of the gastric mucosa was compatible with the hunger contractions of the empty stomach. This

may explain why entrance of bile or intestinal juice into the stomach produces little or no effect on the hunger activity unless the concentration becomes sufficiently high to effect the usual inhibition.

All acids, or liquids containing acids, including normal gastric juice, cause inhibition of the movements and the tonus of the empty stomach when introduced directly into the stomach cavity. In the monkey, the introduction of 5 to 10 cc. of 0.5 per cent. hydrochloric acid directly into the stomach is more effective than the alkali, producing complete inhibition of the movements of the empty stomach. The duration of this period of acid inhibition varies from twenty to forty-five minutes or more and is probably determined by three factors, namely, (1) passing of the acid into the duodenum, (2) fixation and neutralization of the acid by the mucous gastric secretion, (3) neutralization by bile and intestinal juice, which at times pass into the stomach through the dilated pylorus. Normal gastric juice of full normal acidity (0.48 to 0.53 per cent.) and other acid solutions inhibit the hunger contractions, but it does not follow that a neutral or alkaline reaction in the stomach cavity is a prerequisite for these contractions, because, as pointed out by Carlson (*43*), the contractions reappear again before all the acid has passed out of the stomach or has been completely neutralized. In other words, the hunger contractions are not inhibited by weak concentrations of acids in the stomach, nor is it necessary for the gastric mucosa to show a neutral or alkaline reaction. In fact, it is now believed that the hydrochloric acid of the gastric juice constitutes the stimulus that leads to the inhibition when the concentration of the acid rises to too high a level of concentration. None of these substances has been introduced into the mouth or the intestine to determine their influence on the motor activity of the empty stomach of the monkey.

Mechanical stimulation (tickling) of the pads of the feet, posterior limbs, when the animal is asleep, causes a slight fall in the amplitude or strength of the hunger contractions (Fig. 82 B). This result, however, establishes the possibility of a reflex action over the afferent fibers of the sciatic nerve, which is capable of influencing the gastric activity.

Reflex Inhibition by Mechanical Stimuli

Reflex or psychic inhibition of the hunger contractions appears whenever an animal is annoyed, angered or frightened, or whenever cerebral processes of strong emotions or pleasure are involved, such as the entrance of a friend (animal keeper) into the room. In this connection the influ-

ence on the hunger contractions of the sight and smell of palatable foods was investigated. In Vlcek, when hungry, such psychic stimuli did not seem to affect his gastric hunger contractions, but in certain other human individuals positive reactions have been obtained. In dogs the sight and smell of food lead to temporary inhibition of the hunger contrac-
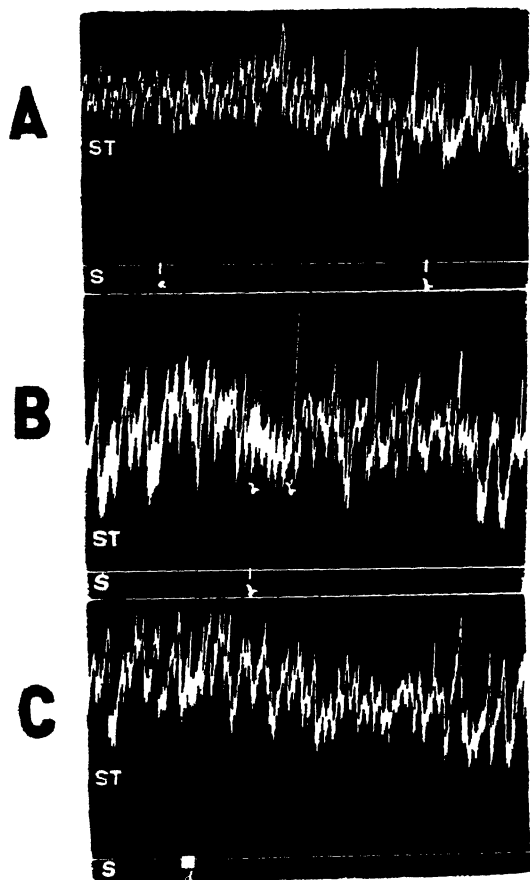

FIG 83.—Monkey III, "Susie." Records from the empty stomach of the young adult after a fast of twenty-five hours, showing the effect of feeding small quantities of food. A, feeding. At *a*, one sunflower seed ; at *b*, two seeds. Note the total absence of inhibition. B, feeding. At *b*, slice of banana. *b* to *b'*, animal chewing. Note the slight inhibition. C, effect of sight of food on hunger contractions. At *d*, animal was shown a banana. Note the slight inhibition in the amplitude of contractions. Water manometer. St, stomach contractions. S, signal. About one-half the original size.

tions, and the inhibition is directly proportional to the degree of interest taken in the food. This is a true reflex or psychic inhibition, since it appears too quickly and is too temporary to be caused by a psychical secretion of gastric juice from the stomach mucosa (acid inhibition). Dogs usually react well to the sight and smell of food during the first few tests, but later, when they learn that they are not to be given the

food, they lose interest and pay little attention to the food shown them, with the result that the hunger contractions are no longer affected by such psychic stimuli. The particular inhibition here illustrated is of the order of "conditioned" reflexes and is similar to Pavlov's (*185*) "psychic" secretion of gastric juice, resulting from the seeing and smelling of palatable food. These reflexes require the presence of hunger and appetite as well as a certain fixation of the attention on the food.

Effect of Feeding Small Quantities of Food

The reaction of the monkey to the sight and smell of palatable food is in confirmation of the statements above, and, on the whole, appears to be more closely related to that of the stomach of man than to that of the dog (Fig. 83 C). The effect of feeding very small quantities of food. such as one, two or three sunflower seeds at a time, does not produce an inhibition of the gastric tonus or hunger contractions (Fig 83 A) but, when larger portions are fed—as, for example, a slice of banana—a definite fall in the gastric tonus and a diminution in the amplitude of the hunger contractions follow, along with the swallowing of saliva (Fig. 83 B). These results on the monkey are in accord with those of Ivy and Vloedman (*98*), who found that in young dogs fasted forty-eight hours, ten to twenty grams of ground, lean sausage caused only a temporary inhibition, corresponding in time and duration to the receptive relaxation of the stomach secondary to deglutition, the hunger period going on to completion in from ten to fifteen minutes. As much as from seventy-five to one hundred grams of the lean sausage were required to cause complete inhibition.

THE GASTRO-NEURO-MUSCULAR MECHANISM

THE NATURE OF THE GASTRIC RESPONSE

Granted that there is a gastro-tonic mechanism, the question logically arises, what controls the production of this tonus, which during life undergoes marked oscillations under various conditions. It is usually considered that an organ becomes atonic after the severance of its extrinsic nerves, but according to Chang (*57*) we cannot regard either the Heidenhain-pouch or the vivi-perfused stomach as being invariably lacking in tone. Although the latter may be expected to possess very little tone following the method of its preparation, this is only temporary, for as soon as the circulation is re-established there is a recovery of tone and the con-

tractions reappear. Chang (57) and Robins and Boyd (197) have also observed a similar type of periodic contractions in the Heidenhain-pouch.

Carlson (44) has shown that complete isolation of the dog's stomach from the central nervous system produces practically a permanent hypotonus of the stomach except under conditions of prolonged fasting, and the author (171) has made similar observations on the bullfrog. In dogs, section of the vagi alone leaves the empty stomach on the whole in a permanent hypotonic condition, at least for a period up to three months after the operation, while section of the splanchnic nerves alone increases the gastric tonus and augments the gastric hunger contractions. In bullfrogs, somewhat similar results have been obtained from partial isolation of the stomach from the central nervous system. In each case, however, there was a complete recovery to normal, following a temporary period of either an increased or decreased tonal activity, depending on the nerves sectioned, whereas after complete section of all extrinsic nerves (vagi and splanchnics), there was only a partial recovery (171). This would indicate in the bullfrog that both the intrinsic and extrinsic nervous mechanisms play an important rôle in the maintenance of gastric tonus upon which the gastric contractions are dependent (204).

Ri (195), working on the innervation of the ileo-cæcal sphincter in rats, has reported that the splanchnic nerve is motor and the vagus is inhibitory in their action on this portion of the alimentary tube. This investigator believes that the Auerbach-Meissner plexus is the functional nervous system which originates the periodic activity of the sphincter, and indicates that the factor of tonus exerts, under certain conditions, a governing influence on its muscular response.

Tonus changes are more marked and occur more frequently during hunger than during normal digestive peristalsis. In most healthy animals in a fasting condition, there is a state of increased tonus in the stomach musculature. Sudden and marked fluctuations in the gastric tonus and less frequently augmentations in the gastric motility have been reported by Carlson (42, 44) in the dog and in man, and such reactions have also been observed in the monkey's stomach. Luckhardt (123) was able to show gastro-tonal changes in dogs during the dreaming state. The author (165, 166, 167) found very marked and abrupt changes in gastric tonus as a result of prolonged fasting, in dogs of different ages, the variations being due to the actual age of the stomach and the correlation of the gastric hunger mechanism with the metabolic gradient or need of food.

Goltz (*86*) found that various types of stimulation, applied to different parts of the frog's skin, led to an increased hypertonus and motility of the stomach. He did not, however, consider these effects as types of reflex activity but assumed that the intense stimuli employed more or less completely paralyzed the medullary center from which, under normal conditions, the tonic inhibitory impulses for the esophagus and stomach arose. These observations were confirmed by Contejean (*58*) and Steinach (*215*). Rogers and Bercovitz (*203*) have stated that in the turtle no method of increasing gastric tonus is available by stimulation of the vagus, their results being either negative or in the direction of a slight inhibition. Von Openchowski (*234, 235*) on stimulation of the kidney, uterus, urinary bladder and sciatic nerve in the rabbit, has reported a reflex dilatation of the cardia.

THE INFLUENCE OF STIMULATION OF THE SCIATIC ON THE TONUS AND MOTILITY OF THE GASTRIC MECHANISM

When both vagi and the sphlanchnic nerves are intact, stimulation of the central end of the sciatic nerve with a weak tetanizing current results in either an augmentation or an inhibition of the stomach, with the characteristic rise in blood pressure. The response appears to be primarily dependent upon the pre-existing state of tonus of the gastric mechanism itself, and may involve both tonus and movement, these varying quite independently of each other. If the stomach is hypertonic and exhibiting contractions, central stimulation of the above nerve will produce a temporary reflex inhibition of the gastric hunger contractions (Fig. 84 A). On the contrary, if the stomach is hypotonic and quiescent, with the exception of the respiratory intragastric pressures, then such stimulation will lead to a decided increase in the gastric tonus (Fig. 84 B).

All of these results are usually not obtained from the same animal, for the state of tonus of the organ may remain more or less constant throughout the course of an entire experiment covering four to six hours; but once in a while an animal will actually show, during the course of an experiment, a distinct fluctuation in gastric tonus. Figure 85 A, B, C and D, shows an animal in which such a change in gastric tonus occurred and the actual time covered was about thirty-five minutes in the four tracings. In this experiment, moderate traction was used on the central end of the sciatic. In figure 85 A the stomach is quiescent and hypotonic. Stimulation by traction results in an increase in the gastric tonus, along with the typical rise in blood pressure. This effect was

obtained several times by such stimulation, previous to this curve, and then without any warning or further stimulation the tonus of the stomach began to increase and, in order to prevent air from escaping through the manometer, it was necessary to open the clip on the instrument to reduce the air pressure in the stomach balloon. This is indicated by the vertical line marked d in figure 85 B. With the establishment of a new
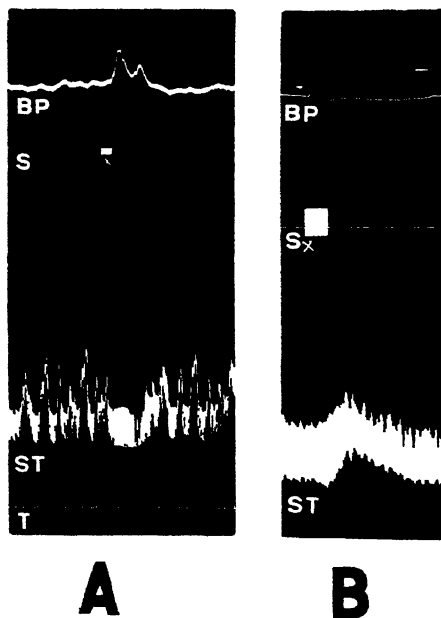

FIG. 84.—Monkey XII. Light ether anesthesia. Vagi and splanchnic nerves intact. A, stomach hypertonic and active. At x, weak tetanizing current applied to central end of left sciatic, producing temporary inhibition of contractions and tonus. B, Monkey XXVIII, stomach hypotonic and quiescent. At x, moderate traction on left uncut sciatic, producing an augmentation in tonus. Note pre-existing state of gastric mechanism determines the type of muscular response. Water manometer. BP, blood pressure. S, signal. St, stomach contractions. T, time in 5 second intervals. About one-half the original size.

tonus level, the stimulation was again repeated with the same effect on the blood pressure but with exactly the opposite effect on the gastric tonus. This means that the stomach had passed from the hypotonic to the hypertonic condition and again, on receiving the same stimulus through the nerve, responded with a fall in gastric tonus (Fig. 85 C). This reaction was obtained throughout the remainder of the experiment, which was continued for about three hours. The last curve (Fig. 85 D) shows the normal level of gastric tonus following recovery from the previous stimulation.

In regard to the effect of sciatic stimulation following section of both vagi in the neck, the author's results on the monkey are, so far negative, but further investigations are under way to check up on this point. However, Wertheimer (238) found that sciatic stimulation caused inhibi-

tion of the stomach and that this reflex was decreased by section of the vagi, but not entirely abolished by subsequent section of both splanchnic nerves.

THE INFLUENCE OF STIMULATION OF THE VAGUS ON THE TONUS AND MOTILITY OF THE GASTRIC MECHANISM

Stimulation of the peripheral cut end of the vagus with a medium tetanizing current produces the characteristic fall in blood pressure, accompanied by a powerful contraction of the stomach, which is then followed by a temporary inhibition of the gastric tonus (Fig. 86 A). The stomach is exhibiting good contractions and may be assumed to be in a medium state of hypertonus. In the next curve the stomach is hypotonic and the weak stimulus, when applied to the nerve, produces a slight fall

FIG. 85.—Monkey XXIII. Light ether anesthesia. Vagi and splanchnic nerves intact. Records showing change in gastric tonus on a quiescent stomach and covering a period of about 35 minutes. A, stomach hypotonic. At x, moderate traction on left uncut sciatic, producing an augmentation in tonus. B, gradual increase in gastric tonus in absence of any artificial stimulus. At d, air pressure in balloon reduced to establish a new tonus level. C, stomach hypertonic. At x, same stimulus applied as in A but producing exactly the opposite effect on the gastric response. D, recovery to normal level of gastric tonus. Water manometer. BP, blood pressure. S, signal. St, stomach contractions. About one-half the original size.

in blood pressure accompanied by a spasm of the stomach and an increase in the gastric tonus (Fig. 86 B). In the third tracing, weak peripheral vagal stimulation in the quiescent hypotonic stomach causes a powerful contraction with a fall in blood pressure. This gastric contraction after a slight fall in tonus is followed by a group of contractions on an elevated tonus level.

If the nerve stimulus is again repeated at x′ exactly the opposite effect now occurs in the stomach, namely, temporary inhibition of contractions with a marked fall in gastric tonus, and the contraction period apparently goes on to completion regardless of its interruption and finally returns to the original tonus level which it possessed previous to the stimulation (Fig. 86 C). This is illustrative of how the gastric tonus, through a given
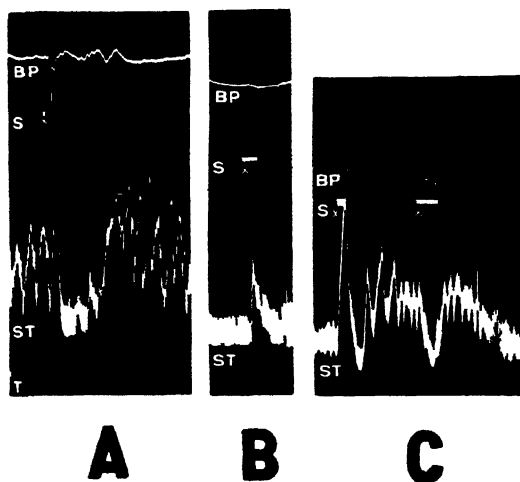

A   B   C

FIG. 86.—Monkey XII. Light ether anesthesia. Vagi cut., A, stomach hypertonic and active. At x, weak tetanizing current applied to peripheral end of right vagus, producing a powerful gastric contraction followed by a fall in tonus. B, Monkey XVI, stomach hypotonic and quiescent. At x, same stimulus applied as in A but producing gastric spasm. C, Monkey XXIV, stomach quiescent and hypotonic. At x, same stimulus applied as in A and B, producing powerful gastric contraction and throwing stomach into period of activity. This is inhibited if the stimulus is again repeated at x′, but there is recovery and the period goes on to completion. Water manometer. BP, blood pressure. S, signal. St, stomach contractions. T, time in 5 second intervals. About one-half the original size.

artificial stimulus, may be increased with the development of stomach motility and then inhibited by a second stimulation of the nerve.

This is in accordance with the work of Rogers and Bercovitz (203), who found that stimulation of the vagus in dogs and turtles may produce either an excitatory effect on gastric motility, or an inhibitory influence on gastric tone and contractions. Brown and Garry (241) made similar observations on the spinal cat from stimulation of the cervical and infracardiac vagus. Langley (117) and May (133) have reported similar results on the rabbit, cat and monkey. More recently, McCrea, McSwiney and Stopford (135) have reported that the primary effect

on the stomach of stimulating the peripheral cut end of either vagus in the rabbit, cat and dog, is dependent on the existing condition of the peripheral mechanism ("tonus") and may be inhibitor or augmentor. The inhibitor or augmentor effect may involve both "tonus" and movement. The final effect of stimulation is to bring about the augmentation of existing movement or to initiate movement. The augmentor response is commonly obtained from the resting stomach, the preliminary
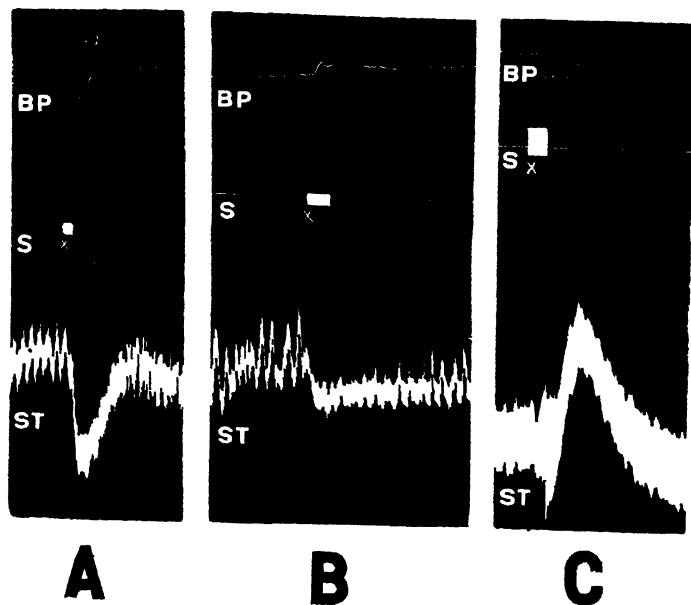

Fig. 87.—Monkey XV. Light ether anesthesia. Vagi and splanchnic nerves intact. Records showing different gradations of gastric tonus with the effect of moderate traction on the uncut vagus. A, stomach strongly hypertonic and active. At x, stimulation of right uncut vagus, producing a marked fall in the gastric tonus. B, Monkey XVI, stomach moderately hypertonic and active. At x, stimulation of right uncut vagus. producing only a moderate fall in the gastric tonus. C, Monkey XXVIII, stomach markedly hypotonic and quiescent. At x, stimulation of left uncut vagus, producing a powerful spasm. Water manometer. BP, blood pressure. S, signal. St, stomach contractions. About one-half the original size.

inhibitor response, from the active digesting stomach two to three hours after a meal. The "tonus" and contraction may vary inversely or directly and the authors think it probable that the entogastric pressure, excitability, and response to stimulation, are governed by the interaction of these various factors which together constitute the peripheral mechanism, and that they are interdependent to a greater or lesser degree.

The mechanism resulting in these effects is peripherally situa.ed, for they occur after bilateral vagotomy. Furthermore, the response of the stomach to vagus stimulation depends not upon the frequency or intensity of the stimulus, as suggested by Veach (230) but upon the condition of the peripheral mechanism (140). The isolated pyloric portion of the stomach also reacts in a similar way (136).

Similar results are also obtained on the monkey when the uncut vagus nerve is stimulated by moderate traction (Fig. 87 A, B and C). In fact, various gradations of tonus are represented in these respective curves with the corresponding effects on gastric motility and blood pressure. By repeated moderate traction on the uncut vagus, in certain ani-
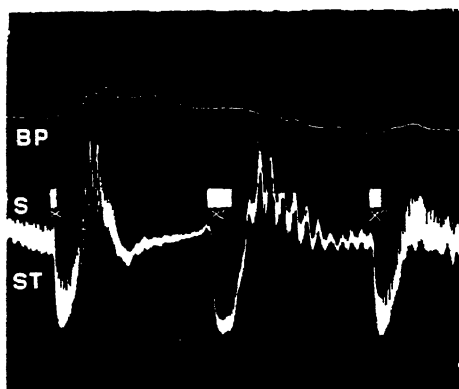

Fig. 88.—Monkey XXIII. Light ether anesthesia. Vagi and splanchnic nerves intact. Stomach in a condition of hypertonus, showing the effect of repeated stimulation by moderate traction on the uncut right vagus at points x, x', x'', respectively. Note the changes in gastric tonus and motility. Water manometer. BP, blood pressure. S. signal. St, stomach contractions. About one-half the original size.

mals, when the stomach is in a condition of hypertonus, it is not only possible markedly to reduce the gastric tonus but also to throw the gastric mechanism into a state of motility for short periods, as is indicated by application of stimulus at x' (Fig. 88). These results offer additional evidence that the response of the gastro-neuro-muscular mechanism is related to the pre-existing state of tonus of the organ, as was suggested by Carlson, Boyd and Pearcy (50) in their explanation of the reflex control of the cardia and lower esophagus. They also obtained both inhibitor and augmentor effects. More recently, Carlson (49) has shown that stimulation of the peripheral end of the hypogastric nerves exerts opposite effects on the ascending and transverse colon. If this portion of the colon is relatively atonic at the time, the stimulation induces a powerful contraction of both the circular and the longitudinal musculature. On the contrary, if this portion of the intestine is in a fair degree of tonus

or rhythmic contractions at the time of the stimulation, the tonus and motility are inhibited.

Does this mean that we are dealing with both inhibitory and motor fibers in the hypogastric, or are these opposite effects produced by one kind of efferents, the specific effect depending on the tonus or motor state of the intestine at the moment of stimulation? Before this question can be satisfactorily answered, we need to have a more correct physiological analysis of the specific action of the fibers of the nerve trunk concerned with such reactions.

Experimental stimulation of the central end of the cut vagus, with the opposite nerve intact, probably produces effects on the gastric response similar to those caused by sciatic and peripheral vagus stimulations and therefore more or less dependent on the pre-existing state of tonus of the gastric mechanism. In support of this, however, Morat (*149*) has obtained inhibition of the stomach on stimulation of the central end of one vagus, provided the other vagus remained intact. After section of both vagi, the author has been unable to elicit this reflex but the work is not fully completed as yet on this particular phase of the question. Laughton (*118*) has recently shown that faradic stimulation of the cephalic half of the dorsal vagus nuclei of the cat causes contractions in the stomach; although, if the organ is hypertonic at the time of stimulation, inhibition of tone results. The cephalic half of the left dorsal vagus nucleus gives a more marked effect on the stomach than stimulation of the corresponding part of the right dorsal vagus nucleus, which is in accord with the findings of McCrea, McSwiney and Stopford (*135*) that the left vagus gives a greater response than that of the right nerve.

THE INFLUENCE OF STIMULATION OF THE SPLANCHNICS ON THE TONUS AND MOTILITY OF THE GASTRIC MECHANISM

The splanchnic nerves are almost universally stated to be the inhibitor nerves of the stomach, but at times various investigators have noted augmentor effects. These nerves were isolated through a skin incision extending from the lateral edge of the deep muscles of the back medially and ventralward for about two inches. By this method the nerves were isolated outside of the peritoneal membrane after passing through the crura of the diaphragm, so that entrance into the abdominal cavity was not required for the exposure of the nerves for stimulation, a factor which is of great physiological importance in this type of experimentation. Van Braam-Houckgeest (*229*), Courtade and Guyon (*60*),

and Klee (112), working on rabbits, cats and dogs, have obtained in-
hibitory effects on the stomach from stimulation of the splanchnic nerves.
Oser (162), in dogs, obtained a weak contraction followed by a relaxa-
tion. Von Openchowski (234, 235) found that stimulation of the splanch-
nic minor with the vagi intact led to a reflex dilatation of the cardia in
the rabbit. Battelli (11), in rabbits, cats, dogs and rats, obtained mostly
inhibitory effects, but a few of the augmentor type were observed. Morat
(149), in rabbits and dogs, and Doyon (70) and Nolf (156), in birds,
obtained both inhibition and augmentation. Elliot (75), in cats and
rabbits, observed an inhibition of the cardia and a contraction of the
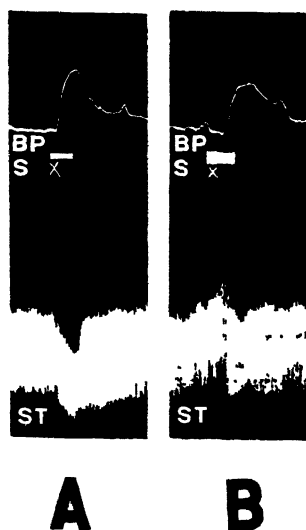
FIG. 89.—Monkey XXIV. Light ether anesthesia.
Records of effect of splanchnic stimulation on
the gastric response. A. stomach hypertonic and
quiescent. At x. strong tetanizing current ap-
plied to peripheral end of left splanchnic, pro-
ducing a fall in gastric tonus with the characteristic
rise in blood pressure. B, same animal, stomach
hypotonic and quiescent. At x, same stimulus ap-
plied as in A but producing exactly the opposite
effect on the gastric tonus with the same blood
pressure reaction as in A. Water manometer.
BP, blood pressure. S, signal. St, stomach. About
one-half the original size.

pyloric sphincter. Carlson, Boyd and Pearcy (50) observed both motor
and inhibitor effects on the cardia and lower end of the esophagus.

In the monkey, stimulation of the peripheral cut end of the splanchnic
nerve with a strong tetanizing current produces the typical rise in blood
pressure accompanied, in some cases, by a fall in the gastric tonus, a
condition probably created by the hypertonic state of the stomach (Fig.
89 A). In the second curve recorded from the same animal thirty-five
minutes later, in which a similar stimulus was employed, there is still
the usual rise in blood pressure, but here again we have just the opposite
effect on the gastric tonus (Fig. 89 B). This rise in tonus is probably
due to the hypotonic state of the gastric mechanism. However, these

reactions from splanchnic stimulation are not as marked as the results usually obtained from stimulation of other nerves already described in the monkey. They are, nevertheless, in general agreement with the published results of McCrea and McSwiney (*13?*) on peripheral splanchnic stimulation in the cat and dog, with the exception that their contractions are very much stronger than any which the author was able to obtain. Stimulation of the central end of the splanchnic seems to exert some influence on the stomach at times, especially in the direction of a reflex inhibition of tonus, but this is another phase of the work which will require special attention for verification.
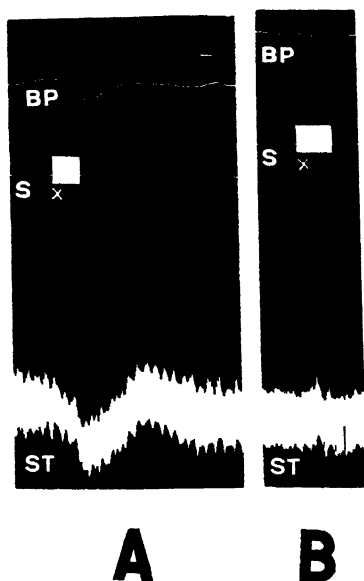
FIG. 90.—Monkey XXVIII. Light ether anesthesia. Vagi and splanchnic nerves intact. Gastric records on the compression of the eyeball—"oculogastric reflex." A, stomach hypertonic and quiescent. At x, moderate compression of the right eyeball, producing an inhibition of the gastric tonus and the blood pressure. B, same animal, stomach hypotonic and quiescent. At x, moderate compression of the left eyeball, producing a slight increase in the gastric tonus and a similar blood pressure reaction as in A. Water manometer. BP, blood pressure. S, signal. St, stomach. About one-half the original size.

THE OCULOGASTRIC REFLEX FROM COMPRESSION OF THE EYEBALL

Compression of the eyeball may exert an influence on the gastric response and is probably dependent, as stated in other parts of this paper, on the pre-existing state of tonus of the peripheral gastric mechanism at the moment of the application of the stimulus. It was not possible to elicit this reflex from all animals studied, but several on which it was tried gave favorable reactions. Moderate compression of the eyeball results in a fall in blood pressure and a fall in the gastric tonus, if the stomach is hypertonic (Fig. 90 A). On the contrary, if the stomach is hypotonic, similar compression of the eyeball may result in a slight in-

crease in gastric tonus along with the usual fall in blood pressure (Fig. 90 B). However, the reflex increase in gastric tonus is much more difficult to obtain than the reflex inhibition of tonus, but it probably exists. These results are confirmatory of those of Daniélopolu and Carniol (*64*) in so far that compression of the eyeballs inhibits the movements of the stomach. It is probable that all afferent sensory nerves of the body may exert a reflex influence on the gastro-neuro-muscular mechanism.

FIG. 91.—Fred Vlcek, the second Alexis St. Martin. Twenty years after permanent closure of esophagus from accidentally drinking a strong solution of caustic potash, which led to establishment of gastric fistula. (Courtesy of Professor A. J. Carlson, The University of Chicago.)

MAN (*Homo sapiens*)

From the standpoint of the development of the stomach, it is generally conceded that it has been evolved from a simple tube, first by an enlargement which is then followed by a bending of the pylorus towards the cardia, and lastly by the addition of one or more cæcal pouches. The pyloric portion of the stomach of Ariolimax (Fig. 18), and the stomach of the eel, consists almost entirely of such a pouch, which has grown from the convex side of a bend in the original tube. It is, therefore, obvious in such stomachs that the primitive tube is to be found along the lesser curvature. In support of this, Oppel (*160*) and Huntington (*95*) have reported that even the complicated stomachs of ruminants can be resolved

into a series of cæca arranged along the original tube. Furthermore, Keith and Jones (*108*) and Lewis (*119*) have brought forth evidence that the fundus of the human stomach represents such a cæcum which in embryonic life grows out from the greater curvature. Lewis (*119*), from his studies on a 10 mm. human embryo, has shown that the stomach is no longer a simple sac with superior and inferior orifices but is composed of three parts, namely: the expanded, conical lower end of the esophagus, the long tubular antrum (pars pylorica), a little wider than the adjacent
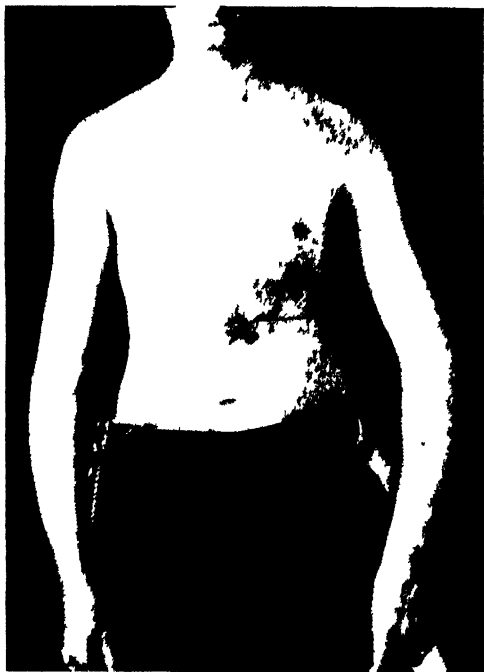
FIG. 92. — Photograph showing permanent gastric fistula of Fred Vlcek, with rubber tube in situ. (Courtesy of Professor A. J. Carlson, The University of Chicago.)

duodenum, and a small fundus. Between the upper and lower portions, and almost exactly in the middle of the stomach, or at the end of the esophagus where it meets the pyloric antrum, is the incisura angularis. The fundus then grows at the expense of the other two parts so that finally, when the stomach has reached its full development, the end of the esophagus is represented only by the cardiac antrum and that prolongation along the lesser curvature which forms the gastric canal. Jefferson (*102*), in his studies on the canalis gastricus, has produced some interesting facts; for many animals, including man, have a loop of muscle fibers along the

lesser curvature which on contracting forms a gutter, or in the ruminants and kangaroos an actual tube. This tube formed by the contraction of the lips of the gastric canal acts as a direct communication from mouth to omasum and abomasum during the period of nursing, but in the adult according to Schalk and Amadon (*210*) it rarely functions in this way. In this manner the primitive tube is largely restored and food is, therefore, prevented from entering the cæcal pouches of the stomach. Further-

FIG. 93.—Photograph of Fred Vlcek, showing arrangement for simultaneous recording of the gastric hunger contractions by the balloon method, and also the vasomotor and cardiac changes by use of the arm plethysmograph. (Courtesy of Professor A. J. Carlson, The University of Chicago.)

more, Wester (*249*) has shown that this rudimentary structure is the starting-point of the peristaltic waves which pass over the reticulum and rumen in one direction and over the omasum in the other, and in confirmation of this Alvarez (*4, 5*) has shown that the most rhythmic tissue in the stomach is to be found on the lesser curvature near the cardia.

No series of comparative studies would be complete without reference to man. The major work on the gastric hunger mechanism on man has been done chiefly by Cannon (*34*) and Carlson (*47*) with the aid of their associates. The writer feels himself most fortunate to have had the rare opportunity of knowing personally, Fred Vlcek, the second Alexis St. Martin, at the University of Chicago, and to have been able to observe directly on him some of this human gastric phenomena. The boy,

Fred Vlcek, at the age of six accidentally drank a strong solution of caustic potash which led to a permanent closure of the esophagus and the establishment of a gastric fistula (Figs. 91, 92 and 93). For a further history of this case the reader is referred to Carlson (*40, 47*).

Furthermore, the writer, in order to become more familiar with the technique as applied to the stomach of the normal human being, has carried out various experiments on himself by the esophageal method and has confirmed many of the physiological states and reactions peculiar to the human stomach as described by these well known investigators. A normal tracing recorded from the fasting stomach of the writer (Fig. 94) at about the age of thirty is shown for comparison with similar curves taken from the fasting stomach of the monkey (see gastric tracings of monkey, Fig. 81 A and B). It should be observed that the contractions of the empty stomach of the monkey are practically identical with those from the empty stomach of man when the factor of age is taken into consideration. An extended discussion of the movements of the fasting stomach of man need not be entered into here, since the important factors bearing on this problem have already been fully discussed in other sections of this paper.

DISCUSSION AND CONCLUSION

The gastric reflexes described in the preceding sections of this paper are reactions depending not only on the condition of the central nervous system, but also on the pre-existing state of the gastro-neuro-muscular mechanism. It must not be inferred that all of these reflexes can be demonstrated in a single animal, even when extreme care is taken with the anesthesia and the trauma of necessary dissections. The reflexes in some specimens were more readily elicited than in others, even under experimental conditions as nearly identical as possible. There is no real explanation to offer for these variations unless they are due to the unknown factor of central and peripheral "shock." In some of the animals a condition of "shock" surely existed, which varied from forty-five minutes to one and one-half hours, during which the breathing might be shallow and the blood pressure very low. However, most of these animals made a good recovery and it was not until then that the actual experimentation was started.

The motor control of the stomach involves local automatism and reflexes via the Auerbach's plexus, long reflexes via the vagi efferents, and long reflexes via the splanchnic efferents. The long reflex mechanisms can

be thrown into activity by the stimulation of such nerves as the sciatic, vagus, and possibly the splanchnic, and it is also probable that stimulation of all sensory nerves throughout the body exerts an influence on the stomach via these mechanisms. Furthermore, the gastric response in these reflexes may be either relaxation or contraction, depending in large part on the pre-existing state of tonus of the stomach at the time of stimulation. If the stomach is in feeble tonus, the contraction reflex prevails; if it is in strong tonus, the inhibition reflex usually predominates. The inhibitor or augmentor effect may, therefore, involve both "tonus" and movement.
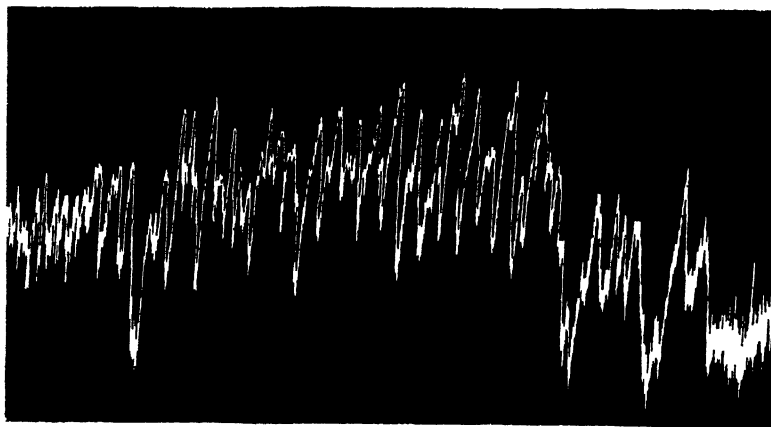
FIG. 94.—Normal hunger contractions from the empty stomach of man (T. L. P., age 81) after a fast of 25 hours. About one-half the original size.

The generally accepted idea regarding the effect of the vagus and splanchnic nerves on the gastro-intestinal tract has been that the vagus carries inhibitory, and the splanchnic motor, impulses to the cardiac and pyloric sphincters, even though reports in the literature varied. Carlson and Litt (52) have shown in dogs that the response of these sphincters to nerve stimulation and to drugs depends upon the physiological condition of the sphincters at the moment the stimulus is applied. If the sphincters are relaxed, the stimulus causes contraction; if the sphincters are contracted, the sphincters are made to relax. Furthermore, McCrea and Macdonald (133) have shown on cats and dogs that the effects produced by the intravenous administration of sympathomimetic (epinephrine, ephedrine, ergotamine) and para-sympathomimetic (pilocarpine, physostigmine, acetylcholine) drugs, like stimulation of the splanchnic or vagus

nerves, vary with the tone of the viscus, but do not closely duplicate the effects of faradic stimulation.   On the other hand, McSwiney and Robson (*141*) and Finkleman (*78*) have advanced some evidence to show that the type of response resulting from vagus and sympathetic stimulation is determined by the liberation of chemical substances in the periphery. More recently, Thomas· (*224*) has demonstrated that the primary action of epinephrine on the pyloric sphincter of the dog, cat and rabbit, in situ may cause either an increase or decrease of the tonus, the former when the muscle is relaxed and the latter when it is contracted.   This also brings up the interesting question of variations in drug action on the stomach, which, on the basis of this investigation, has its explanation in the vexed question of "tonus."   This merely denotes the state of the peripheral mechanism but it tells us nothing of its etiology.   The above observations explain the discordant results reported in the experimental and clinical literature.   They also show that cardiospasm or pylorospasm may be due to reflexes over either the vagi or splanchnic nerves and indicate that the states of spasm or atonicity may be caused by excess activity of either the vagus or splanchnic efferents, motor and inhibitory. The motor and inhibitory nerve fibers, according to Carlson and Litt (*52*), enter the pylorus by way of both of the vagi and of the splanchnic nerves, thus confirming the work of previous observers.   According to these investigators, there are types of pylorospasm that may be decreased or removed by (1) section of the vagus nerves, (2) section of the splanchnic nerves, (3) stimulation of the peripheral end of these nerves.   There are also states of atonicity of the pylorus that may be relieved by section of the vagus nerves.

Chang (*57*), from experiments on dogs, has made the deduction that the response of the stomach musculature is dependent on the state of interaction of the stimulating and inhibiting factors.   Accordingly, the action of drugs on the intact stomach is supposed either to enhance an existing action rendering the opposing action ineffective, or simply to cause a sufficient increase of one component to upset the equilibrium and thus excite the opposing action into effect.   If true, this would offer an answer to the question, but what relation does tonus or tension of the muscle fiber bear to this state of equilibrium?

According to McSwiney and Brown (*139*), there is an existing relationship between the condition of the tissue and the nature of the response elicited by epinephrine, an inhibitor effect being obtained with the contracted or tonic muscle, and an augmentor response from the long or atonic strip.   Since these effects were obtained after the use of diverse

drugs, some of which are regarded as acting on the parasympathetic system, others directly on the muscle, it would appear probable that the reversal effects reported were due to changes accompanying variations in the conditon of the muscle substance.

Unfortunately there is no absolute measure of tonus, so that it is impossible to distinguish the apparent tone of the organ from the normal, except in a very general way.   Therefore, an organ is believed to be tonic when exhibiting motility and atonic when it is quiescent, but this is not necessarily true as is shown by the author's tracings from the stomach of the monkey. (Fig. 85 B and C; Fig. 88; Fig. 89 A; Fig. 90 A). An examination of these curves obtained during stimulation of the sciatic, vagus, splanchnic and eyeball, respectively, indicate conclusively, according to the methods employed in this investigation, that the stomach may be in a good state of tonus without exhibiting motility.   The author believes it is possible, in acute experiments and by properly graded nerve stimulation, to determine the relative degree of the gastric tonus.

A discussion of the genesis of the hunger contractions would not be complete without a consideration of the chemical factors that may be involved.   In the normal animal chemical changes in the blood as well as nervous impulses from the brain and spinal cord augment or decrease the primary automatism of the gastro-neuro-muscular mechanism in a way to correlate it with the needs of the organism.   In support of this conception, Luckhardt and Carlson (124) found that the gastric tonus and motility in normal dogs were increased by the intravenous injections of blood obtained from diabetic and fasting dogs.   More recently, Tschukitscheff (227) has reported confirmatory experiments and further states that if the blood is drawn from a fasting dog during a gastric rest period, it will augment the gastric motility of the recipient, whereas, if the donor's stomach is active at the time the blood is drawn, a similar injection will inhibit the activity of the recipient's stomach.   These results would indicate the presence of a humoral factor or factors in the blood, which were responsible for changing the functioning of the gastric hunger mechanism.   In support of this, Farrell and Ivy (77) and Ivy (99) have shown that a transplanted gastric pouch (100) in the mammary gland of a dog exhibits hunger periods simultaneously with the stomach proper, which affords good evidence that these contractions are due to some humoral agency.   Furthermore, Bulatao and Carlson (27) have shown that sugar metabolism is in some way related to the humoral agency, since dextrose injected intravenously stops the hunger contractions while insulin augments the hunger contractions.   Quigley and

Templeton (*193*) have emphasized the importance of a hormone in the primary control of motility in the fasting stomach and they indicate that this hormonic substance is not the blood sugar. However, as yet, no specific hunger hormone has been isolated. These investigators have also emphasized the importance of the central nervous system in the modification of this motility.

The action of insulin and dextrose on the hunger mechanism promises to throw additional light on this question. Patterson (*176*), working on the gastric motility of the fasting California giant slug, *Ariolimax californicus,* found that insulin introduced directly into the extirpated stomach which had been placed in oxygenated Ringer's solution, markedly augmented the gastric activity while dextrose exerted the opposite or inhibitory effect. (Results with insulin and dextrose unpublished.) Furthermore, Bulatao and Carlson (*27*) have shown that intravenous injections of insulin into normal fasting dogs increased the gastric tonus and motility and also that subsequent injections of dextrose inhibited this tonus and motility. Similar observations have been made by Cascão de Anciães (*243*), Meyer (*246*) and Roholm (*248*) and found to apply to gastric secretion as well as to motility. Farrell and Ivy (*77*) also have noted that the motility of the transplanted gastric pouch in the dog was inhibited in about five minutes by the intravenous injection of relatively large amounts of dextrose.

Quigley, Johnson and Solomon (*191*), using the triple balloon method have obtained similar results in man, with the exception that dextrose— when introduced directly into the stomach with the balloon distended— does not produce inhibition of the gastric motility; and subsequent investigation has indicated that the solution did not leave the stomach, because of the balloon in the pyloric antrum. When the experiment was modified by collapsing the balloons for ten to fifteen minutes following the dextrose administration, or when the solution was put directly into the duodenum, inhibition resulted. Templeton and Quigley (*220*) also have reported that the intravenous or subcutaneous injections of eight to eighty units of insulin in fasting dogs inhibited the motility and depressed the tone of the Heidenhain-pouch at the same time that the tone and motility of the main stomach was being augmented. On the other hand, the intravenous injection of dextrose was usually without effect on the motility of the pouch, but when dextrose was fed to the animal the pouch motility was inhibited. Furthermore, Quigley and Templeton (*192*) have found that the motility of a pouch made from the pyloric region of the dog's stomach was not appreciably altered by either in-

travenous injections of insulin or dextrose, which they attributed to complete denervation of the pouch.   The action of these substances on the gastric motility in double splanchnicotomized dogs while fasting, is similar to that displayed by normal animals except for a slight increase in the gastric activity.

It has been shown further, by Quigley and Templeton (*193*), that the intravenous or subcutaneous injection of insulin does not increase the motility and tonus of the empty stomach of bilaterally vagotomized dogs and that if the stomach is active the hunger contractions are actually inhibited.   Similar injections of dextrose are actually without effect.   Since the other symptoms of insulin overdosage (convulsions, etc.) occurred in these animals in a normal manner, it is believed that the vagi were concerned in the insulin action on the stomach.   Evidence is therefore afforded that insulin acts centrally to augment the discharge of augmentatory impulses over the vagi in the normal animal, since the augmentation of gastric tonus and motility is completely abolished by bilateral vagotomy, the dorsal vagus nucleus possibly acting as the controlling center (*118*).   It is further suggested by these investigators that the gastric inhibition from insulin in vagotomized dogs is probably the result of the stimulating action of insulin on the sympathetic system, thus increasing the inhibitory impulses to the stomach.   The same explanation is offered for the inhibition of the Heidenhain-pouch.   It is also possible that this inhibition may have been produced by a discharge of epinephrine, since Cannon, McIver and Bliss (*37*) have observed that such a discharge occurs when the blood sugar after insulin falls to about seventy mgm. per cent.

La Barre and Destrée (*244*) have recently presented experimental evidence on dogs to show that the increased gastric activity is due primarily to a low blood sugar, which includes not only its muscular but also its secretory activity.   Hence, hypoglycemia following hepatectomy produced about the same effect as insulin, but in both cases the intravenous injections of dextrose in sufficient quantities to raise the blood sugar to normal, or double vagotomy, or atropinisation, immediately abolished the stimulating effect.   However, the inhibiting effect of dextrose occurred only when the blood sugar was low for no such change was ever observed in the gastric activity when the dextrose was given to an intact animal with a normal level of blood sugar, a result which is in confirmation with the experiments of Quigley and Hallaran (*247*).   Furthermore, it has been shown by La Barre (*243*) in cross-circulation experiments that the hypoglycemic blood of one animal when passed through the cerebrum of

a second animal, augmented gastric function in the second even though all connections with the cerebrum were severed save the vagus nerves. This would seem to indicate that the impulses leading to increased gastric activity were transmitted by the vagus and was a result of the blood supply to the brain being low in its content of sugar. If these experiments are confirmed, the rôle of the vagus in the production of hunger and in the augmentation of gastric function will be more clearly under‚ stood.

Granted that the gastric response is dependent on tonus and that increase or decrease of gastric tonus accompanies the gastric augmentation or relaxation, as the case may be, it is suggested that a hypothetical tonus center may exist in the brain, since the administration of insulin in dogs, after complete section of the vagi, results in an inhibition of the gastric tonus and hunger contractions, whereas, in the normal animal, with the vagi intact, there is the usual augmentation in the gastric tonus and motility of the empty stomach (*193*) or possibly the above center may be affected by a low blood sugar to the brain (*243*). It is further suggested that the dorsal vagus nucleus may act as a tonal center for the hollow visceral organs (stomach, intestine, etc.) and be somewhat analogous in its action to that of the vaso-motor center in the maintenance of tonus of blood vessels. It is assumed that, if such a center actually exists, it would be subjected to the varying influences of both nervous and humoral factors of stimulation with efferent connections via the vagi and splanchnic nerves, which would control the tonus and offer a possible explanation for the variations in gastric response from stimulation of such nerves as the sciatic, vagus and splanchnics, as outlined in the earlier sections of this paper.

It should be clear from this discussion that several mechanisms are concerned in the causation of the gastric contractions, which involve the more complicated physiological processes of the tissue elements comprising the gastro-neuro-muscular apparatus. The activity, whether produced by nervous or humoral factors, or both, must in its last analysis be fundamental, the chemical state being altered through changes in isotonicity, nutrition, metabolism, hydrogen ion concentration, cell permeability, etc., upon which, it is assumed, the development of gastric tonus is largely dependent. Such a detailed hypothesis would afford a solution of the question of the reflex coordination existing in the normal physiological state of the stomach and subject to the alterations in the chemical constitution of its tissues, for, until we understand these mechanisms with their underlying basic factors, we cannot expect to be able to analyze and interpret to the fullest extent the handwriting of the stomach.

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ANNALS

OF THE

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THE ORGANIZATION OF THE NEW YORK ACADEMY OF SCIENCES

THE ORIGINAL CHARTER

AN ACT TO INCORPORATE THE

LYCEUM OF NATURAL HISTORY IN THE CITY OF NEW YORK

Passed April 20, 1818

WHEREAS, The members of the Lyceum of Natural History have petitioned for an act of incorporation, and the Legislature, impressed with the importance of the study of Natural History, as connected with the wants, the comforts and the happiness of mankind, and conceiving it their duty to encourage all laudable attempts to promote the progress of science in this State—therefore,

1. *Be it enacted by the People of the State of New York represented in Senate and Assembly,* That Samuel L. Mitchill, Casper W. Eddy, Frederick C. Schaeffer, Nathaniel Paulding, William Cooper, Benjamin P. Kissam, John Torrey, William Cumberland, D'Jurco V. Knevels, James Clements and James Pierce, and such other persons as now are, and may from time to time become members, shall be, and hereby are constituted a body corporate and politic, by the name of LYCEUM OF NATURAL HISTORY IN THE CITY OF NEW YORK, and that by that name they shall have perpetual succession, and shall be persons capable of suing and being sued, pleaded and being impleaded, answering and being answered unto, defending and being defended, in all courts and places whatsoever; and may have a common seal, with power to alter the same from time to time; and shall be capable of purchasing, taking, holding, and enjoying to them and their successors, any real estate in fee simple or otherwise, and any goods, chattels, and personal estate, and of selling, leasing, or otherwise disposing of said real or personal estate, or any part thereof, at their will and pleasure: *Provided always,* that the clear annual value or income of such real or personal estate shall not exceed the sum of five thousand dollars: *Provided,* however, that the funds of the said Corporation shall be used and appropriated to the promotion of the objects stated in the preamble to this act, and those only.

2. *And be it further enacted,* That the said Society shall from time to time, forever hereafter, have power to make, constitute, ordain, and establish such by-laws and regulations as they shall judge proper, for the election of their officers; for prescribing their respective functions, and the

mode of discharging the same; for the admission of new members; for the government of the officers and members thereof; for collecting annual contributions from the members towards the funds thereof; for regulating the times and places of meeting of the said Society; for suspending or expelling such members as shall neglect or refuse to comply with the by-laws or regulations, and for the managing or directing the affairs and concerns of the said Society: *Provided* such by-laws and regulations be not repugnant to the Constitution and laws of this State or of the United States.

3. *And be it further enacted,* That the officers of the said Society shall consist of a President and two Vice-Presidents, a Corresponding Secretary, a Recording Secretary, a Treasurer, and five Curators, and such other officers as the Society may judge necessary; who shall be annually chosen, and who shall continue in office for one year, or until others be elected in their stead; that if the annual election shall not be held at any of the days for that purpose appointed, it shall be lawful to make such election at any other day; and that five members of the said Society, assembling at the place and time designated for that purpose by any by-law or regulation of the Society, shall constitute a legal meeting thereof.

4. *And be it further enacted,* That Samuel L. Mitchill shall be the President; Casper W. Eddy the First Vice-President; Frederick C. Schaeffer the Second Vice-President; Nathaniel Paulding, Corresponding Secretary; William Cooper, Recording Secretary; Benjamin P. Kissam, Treasurer, and John Torrey, William Cumberland, D'Jurco V. Knevels, James Clements, and James Pierce, Curators; severally to be the first officers of the said Corporation, who shall hold their respective offices until the twenty-third day of February next, and until others shall be chosen in their places.

5. *And be it further enacted,* That the present Constitution of the said Association shall, after passing of this Act, continue to be the Constitution thereof; and that no alteration shall be made therein, unless by a vote to that effect of three-fourths of the resident members, and upon the request in writing of one-third of such resident members, and submitted at least one month before any vote shall be taken thereupon.

State of New York, Secretary's Office.

I CERTIFY the preceding to be a true copy of an original Act of the Legislature of this State, on file in this Office.

ARCH'D CAMPBELL,

ALBANY, *April* 29, 1818.   *Dep. Sec'y.*

ORDER OF COURT

THE LYCEUM OF NATURAL HISTORY IN THE CITY OF NEW YORK

TO

THE NEW YORK ACADEMY OF SCIENCES

WHEREAS, in pursuance of the vote and proceedings of this Corporation to change the corporate name thereof from "The Lyceum of Natural History in the City of New York" to "The New York Academy of Sciences," which vote and proceedings appear to record, an application has been made in behalf of said Corporation to the Supreme Court of the State of New York to legalize and authorize such change, according to the statute in such case provided, by Chittenden & Hubbard, acting as the attorneys of the Corporation, and the said Supreme Court, on the 5th day of January, 1876, made the following order upon such application in the premises, viz:

> At a special term of the Supreme Court of the State of New York, held at the Chambers thereof, in the County Court House, in the City of New York, the 5th day of January, 1876:

Present—HON. GEO. C. BARRETT, *Justice.*

In the matter of the application of the Lyceum of Natural History in the City of New York to authorize it to assume the corporate name of the New York Academy of Sciences.

On reading and filing the petition of the Lyceum of Natural History in the City of New York, duly verified by John S. Newberry, the President and chief officer of said Corporation, to authorize it to assume the corporate name of the New York Academy of Sciences, duly setting forth

(Became a law March 19, 1902, with the approval of the Governor. Passed, three-fifths being present.)

The People of the State of New York, represented in Senate and Assembly, do enact as follows:

SECTION I. The Corporation incorporated by chapter one hundred and ninety-seven of the laws of eighteen hundred and eighteen, entitled "An act to incorporate the Lyceum of Natural History in the City of New York," and formerly known by that name, but now known as The New York Academy of Sciences through change of name pursuant to order made by the supreme court at the city and county of New York, on January fifth, eighteen hundred and seventy-six, is hereby authorized and empowered to raise money for, and to erect and maintain, a building in the city of New York for its use, and in which also at its option other scientific societies may be admitted and have their headquarters upon such terms as said Corporation may make with them, portions of which building may be also rented out by said Corporation for any lawful uses for the purposes of obtaining income for the maintenance of such building and for the promotion of the objects of the Corporation; to establish, own, equip, and administer a public library, and a museum having especial reference to scientific subjects; to publish communications, transactions, scientific works, and periodicals; to give scientific instruction by lectures or otherwise; to encourage the advancement of scientific research and discovery, by gifts of money, prizes, or other assistance thereto. The building, or rooms, of said Corporation in the City of New York used exclusively for library or scientific purposes shall be subject to the provisions and be entitled to the benefits of subdivision seven of section four of chapter nine hundred and eight of the laws of eighteen hundred and ninety-six, as amended.

SECTION II. The said Corporation shall from time to time forever hereafter have power to make, constitute, ordain, and establish such by-laws and regulations as it shall judge proper for the election of its officers; for prescribing their respective functions, and the mode of discharging the same; for the admission of new members; for the government of officers and members thereof; for collecting dues and contributions towards the funds thereof; for regulating the times and places of meeting of said Corporation; for suspending or expelling such members as shall neglect or refuse to comply with the by-laws or regulations, and for managing or directing the affairs or concerns of the said Corporation: and may from time to time alter or modify its constitution, by-laws, rules, and regulations.

SECTION III. The officers of the said Corporation shall consist of a president and two or more vice-presidents, a corresponding secretary, a recording secretary, a treasurer, and such other officers as the Corporation may judge necessary; who shall be chosen in the manner and for the terms prescribed by the constitution of the said Corporation.

SECTION IV. The present constitution of the said Corporation shall, after the passage of this act, continue to be the constitution thereof until amended as herein provided. Such constitution as may be adopted by a vote of not less than three-quarters of such resident members and fellows of the said New York Academy of Sciences as shall be present at a meeting thereof, called by the Recording Secretary for that purpose, within forty days after the passage of this act, by written notice duly mailed, postage prepaid, and addressed to each fellow and resident member at least ten days before such meeting, at his last known place of residence, with street and number when known, which meeting shall be held within three months after the passage of this act, shall be thereafter the constitution of the said New York Academy of Sciences, subject to alteration or amendment in the manner provided by such constitution.

SECTION V. The said Corporation shall have power to consolidate, to unite, to co-operate, or to ally itself with any other society or association in the city of New York organized for the promotion of the knowledge or the study of any science, or of research therein, and for this purpose to receive, hold, and administer real and personal property for the uses of such consolidation, union, co-operation, or alliance subject to such terms and regulations as may be agreed upon with such associations or societies.

SECTION VI. This act shall take effect immediately.

STATE OF NEW YORK,
    OFFICE OF THE SECRETARY OF STATE.

I have compared the preceding with the original law on file in this office, and do hereby certify that the same is a correct transcript therefrom, and the whole of said original law.

Given under my hand and the seal of office of the Secretary of State, at the city of Albany, this eighth day of April, in the year one thousand nine hundred and two.

JOHN T. McDONOUGH,
Secretary of State.

CONSTITUTION

ARTICLE I. The name of this Corporation shall be The New York Academy of Sciences. Its object shall be the advancement and diffusion of scientific knowledge, and the center of its activities shall be in the City of New York.

ARTICLE II. The Academy shall consist of six classes of members, namely: Active Members, Fellows, Section Members, Affiliated Members, Corresponding Members and Honorary Members. Active Members shall be the members of the Corporation who live in or near the City of New York, or who, having removed to a distance, desire to retain their connection with the Academy. Fellows shall be chosen from the Active Members in virtue of their scientific attainments. Corresponding and Honorary Members shall be chosen from among persons who have attained distinction in some branch of science. The number of Corresponding Members shall not exceed two hundred, and the number of Honorary Members shall not exceed fifty.

ARTICLE III. None but Fellows and Active Members who have paid their dues up to and including the last fiscal year shall be entitled to vote or to hold office in the Academy.

ARTICLE IV. The officers of the Academy shall be a President, as many Vice-Presidents as there are sections of the Academy, a Corresponding Secretary, a Recording Secretary, a Treasurer, a Librarian, an Editor, six elected Councilors and one additional Councilor from each allied society or association. The annual election shall be held on the third Monday in December, the officers then chosen to take office at the first meeting in January following.

There shall also be elected at the same time a Finance Committee of three.

ARTICLE V. The officers named in Article IV shall constitute a Council, which shall be the executive body of the Academy with general control over its affairs, including the power to fill *ad interim* any vacancies that may occur in the offices. Past Presidents of the Academy shall be *ex-officio* members of the Council.

ARTICLE VI. Societies organized for the study of any branch of science may become allied with The New York Academy of Sciences by consent of the Council. Members of allied societies may become Active Members of the Academy by paying the Academy's annual fee, but as members of an allied society they shall be Affiliated Members with the

rights and privileges of Section Members, except the receipt of its publications. Each allied society shall have the right to delegate one of its members, who is also an Active Member of the Academy, to the Council of the Academy, and such delegate shall have all the rights and privileges of other Councilors.

ARTICLE VII. The President and Vice-Presidents shall not be eligible to more than one re-election until three years after retiring from office; the Secretaries and Treasurer shall be eligible to re-election without limitation. The President, Vice-Presidents and Secretaries shall be Fellows. The terms of office of elected Councilors shall be three years, and these officers shall be so grouped that two, at least one of whom shall be a Fellow, shall be elected and two retired each year. Councilors shall not be eligible to re-election until after the expiration of one year.

ARTICLE VIII. The election of officers shall be by ballot, and the candidates having the greatest number of votes shall be declared duly elected.

ARTICLE IX. Ten members, the majority of whom shall be Fellows, shall form a quorum at any meeting of the Academy at which business is transacted.

ARTICLE X. The Academy shall establish by-laws, and may amend them from time to time as therein provided.

ARTICLE XI. This Constitution may be amended by a vote of not less than three-fourths of the Fellows and three-fourths of the Active Members present and voting at a regular business meeting of the Academy, provided that such amendment shall be publicly submitted in writing at the preceding business meeting, and provided also that the Recording Secretary shall send a notice of the proposed amendment at least ten days before the meeting, at which a vote shall be taken, to each Fellow and Active Member entitled to vote.

BY-LAWS

As Adopted, October 6, 1902, and Amended at Subsequent Times

CHAPTER I

OFFICERS

1. *President.* It shall be the duty of the President to preside at the business and special meetings of the Academy and also at the meetings of the Council.

2. *Vice-Presidents.* In the absence of the President, the senior Vice-President, in order of Fellowship, shall act as the presiding officer.

3. *Corresponding Secretary.* The Corresponding Secretary shall keep a corrected list of the Honorary and Corresponding Members, their titles and addresses, and shall conduct all correspondence appertaining to such membership. He shall make a report at the Annual Meeting.

4. *Recording Secretary.* The Recording Secretary shall keep the minutes of the meetings of the Academy and of the Council; he shall have charge of all records of the Academy, and of its corporate seal, which he shall affix and attest as directed by the Council; he shall keep a corrected list of the Active Members and Fellows, and shall send to them announcements of the Meetings of the Academy; he shall notify all Members and Fellows of their election, and members of committees of their appointment; he shall notify the members of the Council of the dates of the meetings thereof; he shall lay before the Council at each meeting all matters which have come to his attention since the last meeting and which require the consideration of the Council.

5. *Treasurer.* The Treasurer shall receive all membership fees and dues, all interest accruing and paid on the invested or other funds of the Academy, and contributions to the Treasury of the Academy from any other source. All such moneys, as received, shall be deposited in Banks or Trust Companies approved and designated by the Council as depositories, in the corporate name of the Academy and subject to the drafts of the Treasurer, as such. All bills and debts against the Academy shall be paid by the Treasurer on the order of the Council for their discharge.

The Treasurer shall report to the Council at each meeting thereof a statement of the current income and expenditures, and at the Annual Meeting, he shall report to the Academy the balance sheet of the funds and the income account for the preceding year.

6. *Librarian.* The Librarian shall have charge of the library, under the general direction of the Library Committee of the Council, and shall conduct all correspondence respecting exchanges of the Academy. He shall make a report on the condition of the library at the Annual Meeting.

7. *Editor.* The Editor shall have charge of the publications of the Academy, under the general direction of the Publication Committee of the Council. He shall make a report on the condition of the publications at the Annual Meeting.

CHAPTER II

COUNCIL

1. *Meetings.* The Council shall hold meetings at such stated times as it may decide upon, or at the call of the President. The Council shall have general charge of the affairs of the Academy.

2. *Quorum.* Five members of the Council shall constitute a quorum.

3. *Officers.* The President, Vice-Presidents and Recording Secretary of the Academy shall hold the same offices in the Council.

4. *Committees.* The Standing Committees of the Council shall be: (1) an Executive Committee consisting of the President, Treasurer, and Recording Secretary; (2) Such other committees as from time to time shall be authorized by the Council.

CHAPTER III

FINANCE COMMITTEE

The Finance Committee of the Academy shall audit the Annual Report of the Treasurer, and shall act with him in the recommendation to the Council of investments of funds of the Academy.

CHAPTER IV

ELECTIONS

1. *Active Members.* (*a*) Active Members shall be nominated in writing to the Council by at least two Active Members or Fellows. If approved by the Council, they may be elected at the succeeding business meeting.

(*b*) Any Active Member who, having removed to a distance from the city of New York, shall nevertheless express a desire to retain his connection with the Academy, may be placed by vote of the Council on a list of Non-Resident Members. Such members shall relinquish the full privileges and obligations of Active Members. (*Vide* Chapters V and X.)

2. *Section Members.* Workers in science may be elected to Section Membership for a period of five years in the manner prescribed for Active Members. They shall not have the power to vote and shall not be eligible to election as Fellows, but may receive the publications. At any time subsequent to their election they may assume the full privileges of Active Members by paying the dues of such Members.

3. *Fellows, Corresponding Members and Honorary Members.* Nominations for Fellows, Corresponding Members and Honorary Members may be made in writing either to the Recording Secretary or to the Council at its meeting prior to the Annual Meeting. If approved by the Council, the nominees shall then be balloted for at the Annual Meeting.

4. *Officers.* Nominations for Officers, with the exception of Vice-Presidents, may be sent in writing to the Recording Secretary, with the name of the proposer, at any time not less than thirty days before the

Annual Meeting. Each section of the Academy shall nominate a candidate for Vice-President, who, on election as such, shall be Chairman of the section; the names of such nominees shall be sent to the Recording Secretary properly certified by the sectional secretaries, not less than thirty days before the Annual Meeting. The Council shall then prepare a list which shall be the regular ticket. This list shall be mailed to each Active Member and Fellow at least one week before the Annual Meeting. But any Active Member or Fellow entitled to vote shall be entitled to prepare and vote another ticket.

CHAPTER V

DUES

1. *Dues.* The annual dues of Active Members and Fellows shall be $10, payable in advance at the time of the Annual Meeting; but new members elected after May 1, shall pay $5 for the remainder of the fiscal year.

The annual dues of Section Members shall be $2, payable in advance at the time of the Annual Meeting.

Non-Resident Members shall be exempt from dues, so long as they shall relinquish the privileges of Active Membership. (*Vide* Chapter X.)

2. *Members in Arrears.* If any Active Member or Fellow whose dues remain unpaid for more than one year, shall neglect or refuse to pay the same within three months after notification by the Treasurer, his name may be erased from the rolls by vote of the Council. Upon payment of his arrears, however, such person may be restored to Active Membership or Fellowship by vote of the Council.

3. *Renewal of Membership.* Any Active Member or Fellow who shall resign because of removal to a distance from the city of New York, or any Non-Resident Member, may be restored by vote of the Council to Active Membership or Fellowship at any time upon application.

CHAPTER VI

PATRONS, DONORS AND LIFE MEMBERS

1. *Patrons.* Any person contributing at one time $1,000 to the general funds of the Academy shall be a Patron and, on election by the Council, shall enjoy all the privileges of an Active Member.

2. *Donors.* Any person contributing $50 or more annually to the general funds of the Academy shall be termed a Donor and, on election by the Council, shall enjoy all the privileges of an Active Member.

3. *Life Members.* Any Active Member or Fellow contributing at one time $100 to the general funds of the Academy shall be a Life Member and shall thereafter be exempt from annual dues; and any Active Member or Fellow who has paid annual dues for twenty-five years or more may, upon his written request, be made a Life Member and be exempt from further payment of dues.

CHAPTER VII

SECTIONS

1. *Sections.* Sections devoted to special branches of Science may be established or discontinued by the Academy on the recommendation of the Council. The present sections of the Academy are the Section of Biology, the Section of Geology and Mineralogy, the Section of Anthropology and the Section of Psychology.

2. *Organization.* Each section of the Academy shall have a Chairman and a Secretary, who shall have charge of the meetings of their Section. The regular election of the Secretary shall take place at the October or November meeting of the section and the Secretary-elect shall take office on the January first following. At the time of the election of the Secretary the section shall nominate a candidate for Vice-President of the Academy, who, on election as such, shall become Chairman of the section. Vacancies in these offices shall be filled pro-tempore by vote of the section; a chairman so elected being thereby nominated to the Council of the Academy for election as a Vice-President.

3. *Affiliation.* Members of scientific societies affiliated with the Academy, and members of the Scientific Alliance, or men of science introduced by members of the Academy, may attend the meetings and present papers under the general regulations of the Academy.

CHAPTER VIII

MEETINGS

1. *Business Meetings.* Business meetings of the Academy shall be held on the first Monday of each month from October to May inclusive.

2. *Sectional Meetings.* Sectional meetings shall be held on Monday evenings from October to May inclusive, and at such other times as the Council may determine. The sectional meeting shall follow the business meeting when both occur on the same evening.

3. *Annual Meeting.* The Annual Meeting shall be held on the third Monday in December.

4. *Special Meetings.* A special meeting may be called by the Council, provided one week's notice be sent to each Active Member and Fellow, stating the object of such meeting.

CHAPTER IX

ORDER OF BUSINESS

1. *Business Meetings.* The following shall be the order of procedure at business meetings:

1. Minutes of the previous business meeting.
2. Report of the Council.
3. Reports of Committees.
4. Elections.
5. Other business.

2. *Sectional Meetings.* The following shall be the order of procedure at sectional meetings:

1. Minutes of the preceding meeting of the section.
2. Presentation and discussion of papers.
3. Other scientific business.

3. *Annual Meetings.* The following shall be the order of procedure at Annual Meetings:

1. Annual reports of the Corresponding Secretary, Recording Secretary, Treasurer, Librarian, and Editor.
2. Election of Honorary Members, Corresponding Members, and Fellows.
3. Election of officers for the ensuing year.
4. Annual address of the retiring President.

CHAPTER X

PUBLICATIONS

. *Publications.* The established publications of the Academy shall be the *Annals* and the *Memoirs*. They shall be issued by the Editor under the supervision of the Committee on Publications.

2. *Distribution.* One copy of the established publications shall be sent to each Benefactor, Patron, Donor, Life Member, Active Member and Fellow.

3. *Publication Fund.* Contributions may be received for the publication fund, and the income thereof shall be applied toward defraying the expenses of the scientific publications of the Academy.

CHAPTER XI

GENERAL PROVISIONS

1. *Debts.* No debts shall be incurred on behalf of the Academy, unless authorized by the Council.

2. *Bills.* All bills submitted to the Council must be certified as to correctness by the officers incurring them.

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THE MATING BEHAVIOR OF LIZARDS; ITS BEARING ON THE THEORY OF SEXUAL SELECTION*

By G. K. NOBLE AND H. T. BRADLEY

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INTRODUCTION

It is well known that the males of many species of lizards are more brightly colored than the females and some are equipped with gaudily tinted dewlaps, dorsal crests or other structures which, as Cope (1900) conservatively remarks, "are probably visible to the females at the time of copulation. . . ." In view of the many studies dealing with the courtship of birds, it is surprising that the significance of these sexual differences in the courtship of lizards has not received further attention.

DIVERGENT INTERPRETATIONS OF THE SIGNIFICANCE OF BRIGHT COLORS IN THE MALE

Some reference to the mating behavior of lizards is scattered through the herpetological literature but few of the observers have attempted to correlate their observations or interpretations with the work of others. At the present time there is no generally accepted conclusion as to the function of the adornments of male lizards.

It is sometimes assumed that the bright colors of the male lizards serve to stimulate the female. Pycraft (1914), in his general work on the courtship of animals, notes: "It is among the most vividly colored males that most animated displays take place when the endeavor is being made to excite the amorous instincts of the females." On the other hand, Mertens (1926) suggested that the brilliant dewlap of the male *Anolis* might serve as a mechanism for attracting females to their own species. Since each species of *Anolis* in certain regions usually has a distinctively colored dewlap, Mertens argued that the color would aid the female in recognizing males of her own species. Strecker (1928) ac-

cepted this conclusion, which had also been expressed by other naturalists, and added that in his own experience females were "several times observed to approach males while they were making their display." Mertens (op. cit.), however, noted that the male often spreads his throat sac when another lizard is in the vicinity, and added (translation): "One gets the impression that *Anolis* wishes to frighten his neighbor." Any approach of the female *Anolis* which he or Strecker may have observed might also be accounted for in other ways. Mertens (op. cit.) remarks that the possession of such a brightly colored throat sac may work for the ruination of its possessor, since lizards of other species may snap at it, mistaking the sac for an insect.

Still another interpretation as to the significance of bright colors in male lizards has been given by Rose (1929) in describing the south African *Agama atra*. In regard to the male he states: "Certainly his brilliant blue head and light vertebral stripe were calculated to attract the attention of any hovering hawk from his stone-colored better half." This conclusion is apparently based on his earlier observations (Rose, 1926), which seemed to show that the male may remain near at hand during the nesting procedure and, since he is more brilliantly colored than the female, would tend to direct attention to himself and away from her.

It is possible that the bright colors or other secondary sexual characters may have several functions but there are at present in literature very few recorded observations which show conclusively that they have any function at all. For example, *Sitana,* which Pycraft (op. cit.) considered an extreme case of sexual dichromatism, has recently been studied in the field by Gnanamuthu (1930), who noted that, when the males were displaying, no females were visible. Similarly Barbour (1926) has failed to see any sexual function in the dewlap display of *Anolis.* Another naturalist with years of field experience to his credit has bitterly denounced the sexual selection theory as applied to lizards. He states (Wall, 1922) in regard to *Charasia dorsalis:*

The brilliancy of colour appears to be a demonstration of excitement, and, as in many other lizards, is only exhibited by the male. Some naturalists would have us believe that, as in the case of brilliant plumage in birds, it has been evolved by natural selection, the female selecting the male as her mate who has the most brilliant display at his command. This beautiful theory is on a par with a great many other theories elaborated with great ingenuity by modern naturalists. It is pure nonsense in the case of lizards, and if so in lizards, why not in birds? The fact is that with lizards the females make no choice. I have witnessed on many occasions the act of mating among many lizards, especially those of the genus *Calotes,* many of which display very brilliant colours. The male with flaming head (in the case of *C. versicolor*) on sighting

a female rushes upon her. She scuttles away as fast as she knows how, but is overtaken, overpowered and ravished in the most flagrantly brutal fashion. In such circumstances, how can the flaming head be claimed as a lure or charm? On the contrary, past experience must make this a warning colour to the female, and obviously does, because she flees precipitately before it.

THE SCOPE OF THE PRESENT STUDY

In view of this lack of agreement as to the function of even the most striking sexual differences of lizards, it seemed to us highly important to examine the courtship of a series of species including both forms with a marked sexual dichromatism and forms without.

As noted in a preliminary report (Noble and Teale, 1930) this study has led us to some unique conclusions. In the present paper we intend to report in greater detail the evidence on which these conclusions are based.

THE MATING BEHAVIOR OF LIZARDS

TEIIDÆ

AMEIVA CHRYSOLAEMA UNDER LABORATORY CONTROL

The first species which we studied under laboratory control was the active teiid lizard, *Ameiva chrysolaema*. Large numbers of this species were sent to us from Monte Cristy, Santo Domingo. A series of healthy individuals was under our observation from February 1929 to August 1932. These specimens were received in several lots between these dates but we have kept some individuals more than two years in good condition. Most of the lizards were maintained in glass-sided, screen-topped cages, 62.5 cm. long, 40 cm. wide, and 47.5 cm. high (Fig. 1A). Several individuals of both sexes were always placed together in a single cage. The lizards were fed a wide variety of food but the diet which proved to be the most satisfactory was a mixture of certain proportions of raw chopped meat, raw eggs, ground puppy biscuit, yeast, cornstarch and cod-liver oil. This mixture was given them twice a week. Once a week they received canned tomatoes with cod-liver oil, and several times a week a few meal worms (*Tenebrio*) or wax worms (*Galleria*) were thrown into each cage. They decidedly preferred the meat mixture.

Ameiva chrysolaema proved to be a good species for our first observations since it exhibits very little sexual difference in color. The males usually have a large black spot on the chest, the females a smaller spot of the same color. The spot may be reduced in either sex and it may be entirely absent. The larger individuals tend to have a disproportionately

FIGURE 1.—A.—Observation cages employed in this study. The screen tops permit the effective use of the ultra-violet lamp (left). The bark was made available only to the arboreal species.

B.—The mating posture of *Eumeces fasciatus* represents the most generalized type found in lizards. The male (above) holds the skin of the female's neck tightly in his jaws.

larger chest spot. Some individuals may have a bright salmon wash on the ventral surfaces but this does not appear to be correlated with sex. We identified sex by an examination of the cloacas. If there was any doubt, the hemipenis was partly everted. All breeding males had the femoral organs hypertrophied, the secretion often projecting more than a millimeter beyond the orifice of each gland. In the breeding females the femoral organs are much smaller and the secretion does not protrude. Hence, breeding males may be recognized at a glance by the presence of this series of "combs" along the ventral surfaces of the thighs.

MATINGS OF AMEIVA CHRYSOLAEMA

Ameiva chrysolaema lives in semi-arid regions in the tropical lowlands of Hispaniola. It is interesting that, although the laboratory temperatures fluctuated considerably, our lizards mated in every month of the year except September. Fifty-five copulations were recorded during the period of observation but, in addition, there were many courtships and incompleted matings. This extensive series of observations has shown conclusively that *Ameiva chrysolaema* has a complex mating performance, which it endeavors to follow even under difficult circumstances. Deviations from the procedure are due to interference, immaturity or other factors which may be readily recognized.

The Initial Phase of the Courtship

Sexual activity is always initiated by the male. He begins to rub his cloacal region from side to side on the ground. He repeats this performance at intervals of from a few seconds to a minute and may continue the action for two or three minutes. The rubbing movement is rather slow compared to the alert lizard's usual quick, bird-like movements of locomotion. This initial phase of courtship has been recorded thirty-two times and probably occurred at every mating, but passed unnoticed by the observer in the laboratory. Every time that this activity was observed, it was followed by an attempt at copulation within the next few minutes. The male goes through his preliminary performance apparently without having seen the females in the cage with him, his eyes often being closed and his back turned to them. In no case was there the slightest evidence that a female stimulated the male to begin this performance.

The Second Phase of the Courtship

In the second phase of the courtship, the male seeks a mate. He may follow either a male or a female of his own species about the cage and he may rapidly transfer his attention from one sex to the other. He
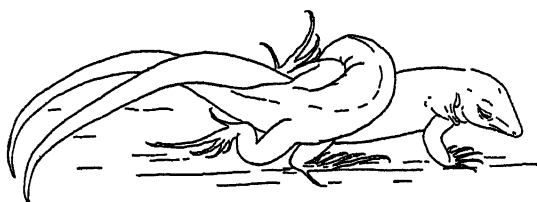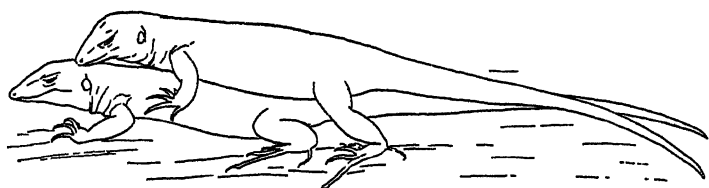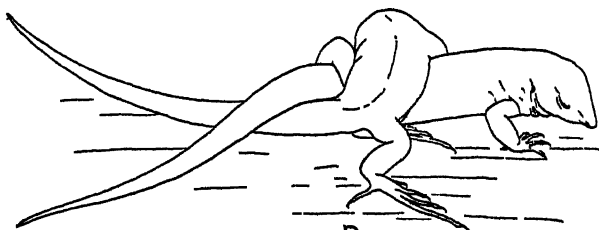
FIGURE 2.—The mating behavior of *Ameiva chrysolaema*.

A.—The male walks above the female while poking her neck with his snout.

B.—When the female becomes quiet, the male slips to one side, arches his body over hers and bites her flank of the opposite side.

C.—The base of the male's tail is brought under that of the female and their cloacas come in contact.

D.—In some cases the male may support his weight with one hind foot but more frequently the legs are flexed as in C.

takes a position directly over the back of his unwilling partner and walks or runs along with his belly lying along his partner's back. The rate of movement depends upon the activity of the partner. If the partner is unusually passive, the courting male does not have to dash about the cage but may lie quietly upon the other lizard's back for a few seconds. If the partner is very active in trying to avoid him, he quickly becomes more active himself and slips immediately into the next phase of the courtship.

The Third Phase of the Courtship

This phase consists of poking the back of his partner's neck with short, quick, but firm nudges of his snout, or nipping the skin in that region. Rarely it consists in both poking and nipping. One or the other action
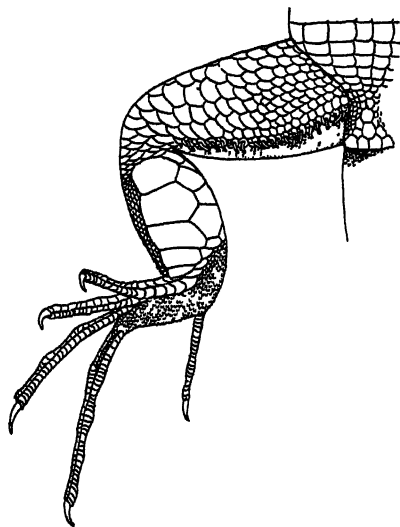
FIGURE 3.—The femoral organs of the male *Ameira chrysolaema* hypertrophy to form a comb which is present in some adult individuals throughout most of the year. The right thigh of a breeding male is viewed above from the ventral aspect.

was recorded in fifty-six cases, but it no doubt occurred in all. The records show that this performance invariably occurs in the same place in the sequence of events; that is, after the male has mounted the female and just before the events about to be described.

While the neck poking is in progress, the cloaca of the courting male gradually swells until the cloacal lips are spread slightly apart. With the swelling of the cloaca the male becomes extremely active, every move-

ment of the limbs and body being accentuated. But a moment later he hesitates as if to give up the neck poking and at the same moment to bring his cloaca near that of his partner. To do this, he drops his pelvic region to one side of his partner and stands on the hind and front feet of one side only. He keeps his other legs pressed against his partner's opposite side and rubs that side vigorously with his hind leg while pressing the upper inner portion of this leg against the skin of her flank just anterior to her thigh (Fig. 2). As already indicated, this part of the thigh is covered with a series of hypertrophied femoral organs (Fig. 3). Unlike the preliminary cloacal movements, this behavior cannot be directed towards self-stimulation because the femoral organs are not sensory but glandular in character. Moreover the rubbing is definitely directed toward quieting the partner. The courting male's hind foot often comes back against or on his partner's leg. Hence the male pushes with his foot while rubbing with his thigh. This action continues for at least three or four seconds. Since the partner usually makes a desperate effort to escape the courting male, the leg rubbing is often repeated several times and kept up until the male finds that his partner is quiet. This may require three or four minutes of desperate rubbing by the courting male. During the rubbing the male extends his tail under that of his partner from the side adjacent to his body to the side which he is rubbing (Fig. 2).

Copulation

Suddenly the male stops rubbing, arches his body in a semicircle over his partner's body and bites firmly the inguinal region of his partner at approximately the point he was rubbing. At the same moment he pushes his cloaca up to his partner's and inserts the hemipenis of the side adjacent to his mate. The male may approach either the right or left side of his partner but he invariably everts only the hemipenis on the adjacent side.

SUCCESSFUL AND UNSUCCESSFUL MATINGS

In every case where copulation was attempted the flank bite was also attempted. If the chosen mate breaks away in the time between the cessation of rubbing and the taking of the flank bite, the mating is "unsuccessful" in our records. That is, the hemipenis is not inserted. However, when the male has gone so far as to attempt a flank bite, his hemipenis is everted, whether into his partner's cloaca or not. Besides the fifty-five successful matings of *A. chrysolaema,* twelve unsuccessful ones were recorded, and these are distinct from incomplete courtships. Of the fifty-five matings only three are recorded as continuing more than a

minute, the rest of them lasting but a few seconds. During copulation the courting male is quiet while the partner, whether male or female, often struggles to gain freedom. Females never show any interest in the courtship or copulation and, while they may be quieted by the rubbing and the subsequent inguinal bite of the courting male, they never take an active part in facilitating copulation.

During a successful mating, the hemipenis is usually not seen by an observer, for, at the moment it is inserted, the cloacas of the pair are already pressed together and it is usually retracted before the male releases the female. Immediately after retraction the male's cloaca is red and swollen, and is dragged on the ground while the tail is held a little arched until this swelling has subsided. During an unsuccessful mating the hemipenis is seen, for, once it is everted, it is not immediately retracted. If the mate has escaped at the moment of the inguinal bite, the hemipenis is everted in space and may be noted as the animal stands quietly until it is retracted a few seconds later. Whether or not the male has been successful in actually copulating, this everting and retracting of the hemipenis seems to satisfy the requirements of the performance, for no further attempt to copulate is made immediately.

The length of time occupied by the entire procedure, both courtship and mating, varies with the vigor with which the female avoids the male. Twelve successful courtships were recorded to have taken from one to five minutes each. Six successful ones took from five to forty minutes. Most long courtships result in no attempt at mating or in an unsuccessful attempt.

EFFECT OF TEMPERATURE ON COURTSHIPS

Temperature plays an important part in courtships. A certain degree of warmth is necessary to provoke activity of any sort among lizards and this degree must be held for a few hours in order that the animals may become sufficiently lively to include mating in their activities. Thirty-nine courtships or matings of *A. chrysolaema* are reported to have taken place at an average temperature of 79.6° F., (maximum 90°, minimum 73°). The temperature readings are those of the room and not of the lizards. Some of the lowest temperatures at which matings occurred were recorded at a time when the lizards were being irradiated with ultra-violet. The actual temperature of the lizards under these conditions was doubtless higher than that of the room. A sudden change from cold to warm weather frequently induced courting. Also a long ultra-violet ray treatment often initiated it.

THE SEXES NOT DISTINGUISHED BY THE COURTING MALE

It is evident from our records that a courting male, *A. chrysolaema,* does not distinguish between males and females. He courts any lizard of his own species and mates with either a male or a female. There are thirty-three records of males courting both males and females before copulating. While males usually mate with the females, they very often court and copulate with males. The reason for their mating more often with females seems to be that a full grown female is a trifle smaller than a full grown male and is a more convenient size for him to overpower. Furthermore, she is less muscular and is presumably easier to subdue. The males have larger heads than the females, the width of the head at the jowls being somewhat greater. Since neither sex uses his or her teeth in defense, this greater development of the jaws of the male is correlated with his inguinal bite during courtship and not with fighting behavior before mating.

That correspondence of size does not play a rôle in mate selection is shown by the fact that a male when courting a male usually selects one smaller than himself. We have, however, eight records of small males mating with larger ones. No courting male can mate with an animal very much smaller than himself.

On two occasions in April, 1930, one male copulated with another male and in doing so sufficiently aroused the second one so that he immediately turned and went through the complete mating performance, including copulation with the male who had just inserted the hemipenis into his cloaca. On another occasion, in July, 1930, a large and a small male were courting all other lizards in the cage as well as each other. Finally the small male copulated with the large male. During the courting the small male was often poking and rubbing the large male while the latter was poking and rubbing a third lizard—the trio moving about the cage three deep! Records such as these make it clear that courting males of *A. chrysolaema* do not follow females only but seek and attempt to copulate with any member of their species.

We have extended our observations to another species of *Ameiva* and have obtained similar results. The Porto Rican *A. exsul* was employed for this study and three matings were recorded in our small series. The three copulations and five additional courtships occurred in February and April of 1932 at an average temperature of 76° F. (Maximum 78°, minimum 74° F.). The phases in the courtship and the act of copulation were the same as in *A. chrysolaema,* except that the male often attempted to hold the female by the neck skin, although neck poking

also occurred. Coition always lasted less than a minute. Although the three matings were by males with females, in every courtship recorded males courted both sexes indiscriminately.

It was obvious in our study of the courtship of these two species of *Ameiva* that we were dealing with a complex behavior pattern which developed spontaneously in males and which was directed toward other individuals regardless of their sex. We obtained no evidence in our large series of observations that the attacked individual called forth the reaction by any specific behavior. The females exhibit no oestrous behavior which stimulates the male. Not only do males mate with males but we have one record of a male copulating with a female proved by dissection to be sexually immature. This mating occurred on January 29, 1932, the day after the male, a small one, had courted actively two other males,—one much larger than himself.

Once the male had begun his courtship performance, we found it possible to remove logs or other obstructions from the cage without delaying the unfolding of his usual courtship pattern. This was true for recently collected individuals as well as for those held in captivity several months.

RANGE OF VARIATION IN THE COURTSHIP OF AMEIVA CHRYSOLAEMA

There is a certain range of variation in the courtship performance. We have selected from our records of *A. chrysolaema* a series of observations which illustrates some of the more common deviations:—

A Successful Mating of a Male of A. chrysolaema with a Female of that Species

July 17, 1929, 3.45 p.m. Room temperature 84° F.

The first female the male courted was lively and resisted. The second female, a fat one, was passive and the male turned to her. He secured a position directly over her and lay for one or two minutes moving his cloacal region from side to side irregularly. Then he poked at her neck, and put his tail under hers, attempting to bring his cloaca near hers. After three attempts, during which he rubbed her with his leg on the region anterior to her hind leg, he took the inguinal bite and at the same time copulated for approximately six minutes. On leaving the female his hemipenis was visible, partly extended, for a second. He walked around with tail raised and cloaca dragging for a few seconds, and then went to sleep.

An Unsuccessful Mating of a Male of A. chrysolaema with Another Male of that Species

May 28, 1930. Room temperature approximately 80° F.

A young male *A. chrysolaema,* 105 mm. head and body length, courted several larger males and some females. His actions were more ineffective than those of others that have mated, but the pattern was the same. He poked the neck, straddled the mate, rubbed with his leg any part of the mate with which it came in contact, often fumbled and poked the mate's tail instead of the neck, with his snout and finally attempted copulation with a very large male. He bit him across the middle of the back instead of on the opposite flank, and so failed to insert the hemipenis. However, the hemipenis was fully everted for one or two seconds; and then was drawn in. The big male had escaped and this little one was left standing perfectly still with tail arched for six or seven seconds. Then the little male walked away, dragging his cloaca. All the nervousness that he had been showing before the last step of the pattern had left him. The complete performance had consumed about 10 minutes.

A Successful Mating of a Male of A. chrysolaema with Another Male of that Species

July 9, 1931. Room temperature 83° F.

A male of *A. chrysolaema* was found courting another larger male. Neck poking, straddling, leg rubbing as usual. Finally the male put his tail under his mate's tail, the flank bite was made and the cloacas were brought together. Almost immediately the mate rolled over and freed himself. It is certain that the small male's hemipenis was in the cloaca of the other for a second. After being thrown off, the aggressive male stood with cloaca raised and hemipenis everted. After a few seconds he dragged his cloaca and hind legs on the ground while moving about the cage for a minute or more. Then he raised one leg, everted the same hemipenis and folded it in again immediately, and walked quickly and nervously about the cage for a few minutes more, paying no attention to any other lizard.

An Unusual Mating of a Male of A. easul with a Female of that Species

February 16, 1932, 4.20 p.m. Room temperature 76° F.

Courtship lasted ten minutes, and coitus forty-five seconds. The male bit the female's neck skin a great deal and held it most of the time. The male was very small and the female quite large. At intervals he poked

her neck.   There was some leg rubbing this time.   He held her neck
until she lay quiet enough for him to insert his hemipenis.   At the
moment of penetration he turned his body and bit her squarely across
the back.   The unusual position for the copulatory bite seemed to be
due to the comparatively small size of the male.

SUMMARY OF OBSERVATIONS ON AMEIVA

To summarize our observations on *Ameiva,* we may repeat that the male
spontaneously develops a sexual activity, which is directed toward any
individual of his own species regardless of sex but within a certain size
range.   The male attempts to quiet the lizard attacked first by neck
poking or biting, then by a scratching of the back or sides with his femoral
organs.   If the attacked individual slackens its pace, the courting male
immediately attempts an inguinal bite while his tail is swung under his
partner's tail and their cloacas are brought in contact.

It seemed to us that any behavior as complex as this must have evolved
from a simpler pattern.   Since in other groups of vertebrates such as
the salamanders (Noble, 1931) a single type of courtship has been found
to characterize certain natural groups of genera, it seemed to us that the
same might prove to be true for lizards.   In order to test this hypothesis,
we selected for comparison with the above species another teiid lizard
which was easily obtainable but one which showed a marked sexual dif-
ference in color.   This species was *Cnemidophorus sexlineatus.*

CNEMIDOPHORUS SEXLINEATUS

The adult males of *Cnemidophorus* which we have had in this laboratory
had their ventral surfaces tinged with blue, frequently of a very bril-
liant hue.   All adult females which we have seen alive lacked this
tinge and were usually white or gray below.   Although this sexual dif-
ference has been previously noted by others, Burt (1931) considers it
merely a case of individual variation.   This opinion is based primarily
on preserved material.   In formalin fixed material the blue tone is
usually discolored.   From the evidence at hand we assume that the blue
tone characterizes all adult males of *C. sexlineatus* during the breeding
season and serves as a ready means of distinguishing males from females.

The male *C. sexlineatus* is one of the most beautiful lizards employed
by us in these studies.   If brilliant colors actually stimulate female lizards
to mate, it seemed probable that this species would afford some evidence
of it.   We witnessed sixteen successful matings in the series of *C. sex-
lineatus*, which were sent to the laboratory from Mississippi and Georgia.

We also recorded seven unsuccessful attempts at copulation and twelve courtships which were interrupted or discontinued before copulation occurred.   To our surprise we found the courtship and copulation behavior of *C. sexlineatus* essentially the same as that of *Ameiva*.   The same phases in the performance are passed through and in the same order.

COURTSHIP AND MATING OF CNEMIDOPHORUS SEXLINEATUS

In the mating performance of *C. sexlineatus* the male first rubs his pelvis on the ground from side to side.   During this first phase of the courtship he may continue the rubbing while running about in a small figure eight.   Often this is all that happens, but this performance may precede courtship and is definitely a sign of sexual activity in the male. Like the male of *Ameiva* he then chases other lizards, male and female, and bites or pokes their necks.   *Cnemidophorus* is equipped with femoral organs nearly as well developed as those of *Ameiva*, and the same kind of leg rubbing is employed by the male.   After the male has assumed the dorsal position he may continue moving his cloaca from side to side on the female's back.   He puts his tail under that of the female in order to bring their cloacas together.   Copulation takes place simultaneously with the flank bite.   The male assumes an arched position across his partner's back exactly as in *Ameiva* (Fig. 4).

Coitus lasts much longer in this genus than in *Ameiva*.   While with the latter it rarely lasts more than a minute, with *Cnemidophorus* it is usually "unsuccessful" if it does not last several minutes.   After being in coitus a few seconds, or rarely after one or two minutes, the male often begins forward thrusts of the pelvic region, forcing forward the inserted hemipenis convulsively.   The thrusts are usually at the rate of about two a second.   This may keep up for minutes.   The female *C. sexlineatus* usually does not struggle once the flank bite has been taken by the male.

The coition of successful matings lasts from five to fifteen minutes although two cases of thirty and forty seconds respectively seemed successful.   A shorter coition than this is unsuccessful due to the escape of the female and, even though the hemipenis has for a moment been in the cloaca of the female, it usually remains everted a few minutes, the male retaining his arched position and going through the usual convulsive movements in mid-air.   Matings occurred at an average temperature of 82.2° F. (maximum 89°, minimum 77°), and four of them immediately followed ultra-violet treatment.

As with *Ameiva*, courting males make no discrimination between the
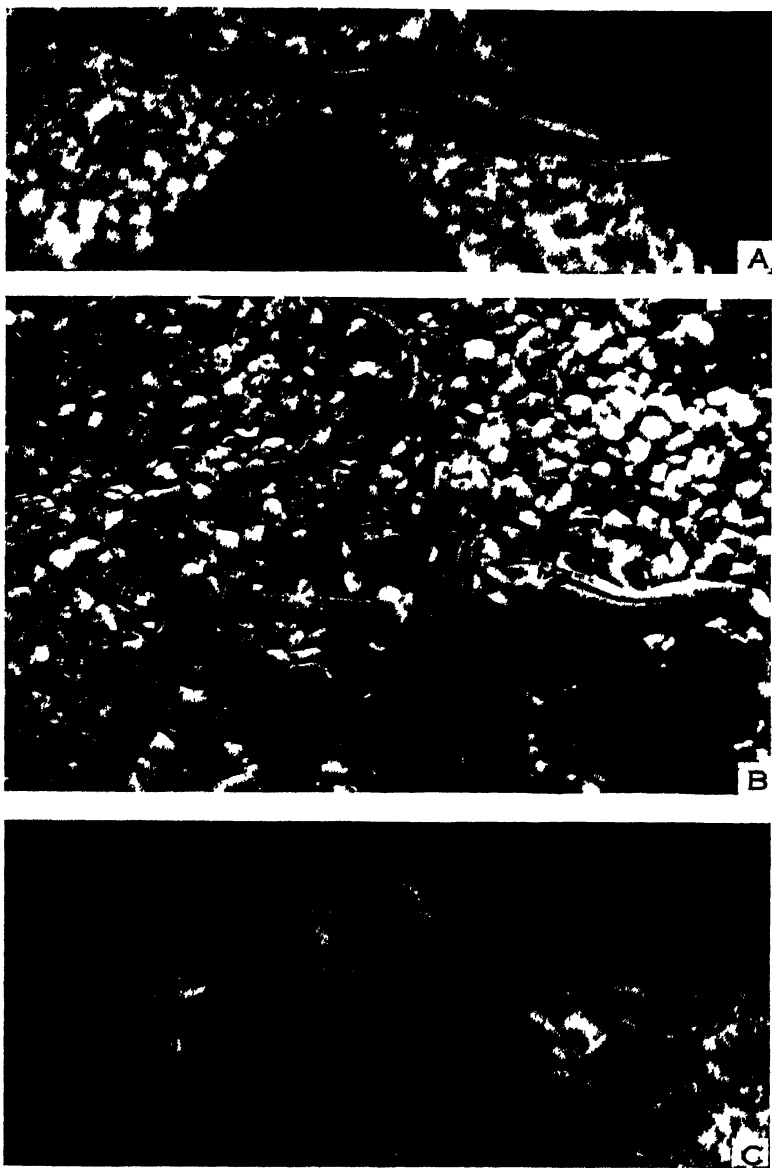
FIGURE 4.—The mating behavior of *Cnemidophorus sexlineatus* is essentially the same as that of *Ameiva*.
A.—The male not only pokes but frequently bites the neck of the female.
B.—The male attempts to secure the flank bite while bringing his cloaca forward.
C.—The flank grip is usually maintained for a much longer period in *Cnemidophorus* than in *Ameiva*.

sexes. There are eight recorded matings or attempted matings of males with males, and seven with females. The other six records are incomplete in regard to this detail.

The courtship and mating of *Cnemidophorus* proceed, as shown above, almost exactly as in *Ameiva,* in spite of the fact that in *A. chrysolaema* there is no constant sexual difference in color while in *C. sexlineatus* the brilliant blue undersurfaces must be partly visible to the female during these acts.

CORRELATION BETWEEN DISPLAY AND FIGHT REACTION

The brilliant livery of the male of *C. sexlineatus* obviously plays no rôle in the mating behavior. The bright tones seem to have other functions and, while our observations are not sufficiently numerous to establish this fact for *Cnemidophorus,* the evidence available may be presented here. The male *C. sexlineatus* equipped with his bright colors differs remarkably from *Ameiva* in that he fights. Evidence will be presented below to show that color displays form a very essential part in the fighting behavior of many lizards. In *C. sexlineatus* the fighting is not frequent. However, the male rises high on his legs to show off his bright colors at that time. In brief, while no correlation exists between courtship and display, a very definite relation is found between fight and display. Two of our records will serve to illustrate this fact.

Aggressive Behavior of a Male of C. sexlineatus

October 20, 1931, 2 p.m. Room temperature 80° F.

A healthy male *C. sexlineatus* chased other lizards of the same species in his cage and bit them savagely across the snout and about the neck, taking the whole head or neck into his jaws. Before biting he rose high on his legs, showing his bright blue ventral surfaces, and with head lowered rushed at his opponents and gripped them. The attacked animal always escaped by shaking himself loose or by rolling over and over, taking with him the fighting male until the grip was loosened and he could escape. This performance was not courtship, for it was much more vigorous than courtship, and a courted animal is grasped by the neck skin, not by the whole neck or snout. Also the attacking male never rubbed his cloaca on the ground and there was no neck-poking and no leg-rubbing. It was impossible, in the general scramble, to tell whether or not the male chased and bit only males or females as well as males.

The Combat of Two Males of C. sexlineatus

October 24, 1931, during the morning treatment of ultra-violet. Room temperature approximately 80° F.

Two males faced each other, with the middle of their backs raised and their heads lowered, tails quivering. They rushed at each other, each trying to bite the head of the other. One finally caught the other under one side of the neck and held on. The under male lay upside down with his eyes closed. After six minutes their breathing became slower and they separated, neither lizard having injured the other.

These fights did not occur on days when there was also courtship. This may be taken as further evidence that the fighting response, so evident in species to be discussed below, has no relation to the courting behavior.

ATTEMPT TO DETERMINE SENSE ORGANS ESSENTIAL TO COURTSHIP

We have attempted by experimental methods to determine what sense organs are essential to the courtship performance. None of our attempts were successful because the elimination of any sense organ sufficiently disturbed the courting male to prevent a completion of the act. Blindfolding courting male *Cnemidophorus,* or placing strips of adhesive tape across the symphysis of the lower jaw, both prevented a continuation of the performance. Handling alone did not prevent the courtship from *continuing* shortly after the male was released. Although the male of *C. sexlineatus* is usually markedly more brilliant than the female, this fact does not appear to aid the courting male in sex recognition. Probably vision is the most important sense in the courtship, but the ability of *C. sexlineatus* to distinguish between the sexes through vision apparently does not exist. This impression is based on our detailed observation of the series of courtships summarized above.

In conclusion we may quote one of our records:—

A Typical Mating in Cnemidophorus sexlineatus

November 16, 1931, 12.05 p.m. Room temperature, approximately 83° F.

A short ten-minute treatment of ultra-violet sexually stimulated a male. He courted various animals in the cage, both male and female; he also rubbed his cloaca on the gravel by moving his hips quickly from side to side as he wiggled through his figure eight. After riding the backs of various animals and occasionally nipping their neck region

(or, in his excitement, other regions of the body), he found a female which did not strenuously resist his courting. He rubbed his hind leg along her lower back and made an effort to place his tail under hers. He finally succeeded, and as their cloacas came together he bent his body in an inverted "u" and bit the female just anterior to the hind leg on the side opposite to that along which he lay. His jaws, wide open, took in half her body thickness. At the same time the hemipenis was inserted. After this the female stopped moving. The male's respiration quickened. Copulation lasted five minutes. Finally the female began moving, dragging the male, in his arched posture, with her. Then she escaped and after a few seconds they each rubbed their cloacas on the ground.

On an earlier occasion, in 1929, a male even before pursuing other individuals had rubbed his cloaca on the gravel by moving his hips quickly from side to side as he ran back and forth in a figure eight. He then courted both males and females and eventually copulated with a female. From this it is evident that the male begins his sex activity without stimulation from the female. The preliminary activity of the male in question followed a ten-minute treatment with ultra-violet.

LACERTIDÆ

Ameiva and *Cnemidophorus* resemble superficially the Old World lizards of the genus *Lacerta*. The courtship of *Lacerta* has been more extensively studied than that of any other group of lizards. It is, therefore, interesting to compare the sexual behavior of these long-snouted lizards because, if body form has an influence on the courtship pattern, their mating performances should be very much alike.

COURTSHIP AND MATING OF LACERTA MURALIS

One of the earliest accounts of the mating of *Lacerta muralis* is that of Gachet (1833), who correctly reports that the female, although in a breeding condition, does not yield to the male until she has been subdued by him. The male seizes the female in his jaws and is dragged about for a time until the cloacas are brought in contact. Glückselig (1863), Collin de Plancy (1877) and Rollinat (1897) have added important details to the picture. They show that the performance proceeds on a different plan from the teiids described above. The male usually bites the female in the tail and, when she has become quiet, he lets go the tail and seizes the female in the flank immediately anterior to the hind limbs. Then he brings his body forward in a semicircle toward the female until

their cloacas are in contact.   The male does not employ his femoral organs to quiet the female with rubbing movements and he does not arch his body over hers.   Copulation is accomplished with the hemipenis on the side adjacent to that which he has bitten.   There is nothing in these earlier accounts to justify the statement of Romanes (1883) that:

> The male, during the spring of the year, exhibits great attachment towards the female.   Throwing aside his usual gentleness of character he defends her even with fury, attacking with undaunted courage every animal that seems inclined to injure her. . . .

The mating performances of other species of *Lacerta* are essentially the same as that of *L. muralis,* indicating that there is a stereotyped performance in this genus which is closely adhered to by all the species so far as known.   Glückselig (1863) reports a male of *L. muralis* attempting to mate with another male but no observers have described the males of any species of the genus selecting partners regardless of sex.   One explanation for this may be that the observers may have assumed that a lizard which permitted the insertion of a hemipenis into its cloaca must be a female.   Before we had definitely established that the male of *Ameiva* often submits to the passive rôle in copulation we, also, had assumed such individuals to be females.

THE MATING BEHAVIOR OF LACERTA AGILIS

One phase in the courtship of *Lacerta* requires further consideration. Glückselig (op. cit.) reported the female of *Lacerta viridis* and of *L. muralis* as responding to the approach of the male lizards with rapid movements of their forelimbs.   In *Lacerta agilis,* which exhibits a marked sexual dimorphism of color, Klingelhöffer (1900) describes a similar movement as a drumming behavior intended to attract the attention of the males.   Klingelhöffer also reports contractions of the body of the female for about 1 cm. before and behind the cloaca.   These contractions are rhythmical at the rate of approximately 150 a minute and they may extend part way down the tail.   These contractions, Klingelhöffer reports, may be elicited by the sight of the male, and sometimes by touching the female's back with a feather.   He states that it is not unusual to see all the females lying in the sun and undergoing these cloacal contractions.   Klingelhöffer also describes the females as dashing at the males and attempting to hold them with their jaws.   Thirty-one years later Klingelhöffer (1931) has described this courtship again, introducing very little change in his description.   This account, if correct, would

indicate that the female of *L. agilis* experiences an incipient form of oestrus which induces her to attract the attention of the male.

Mortensen (1887), on the other hand, describes the mating behavior of *L. agilis* as essentially like that of *L. vivipara,* which he reports in great detail without reference to any aggressive action on the part of the female. Moreover, he definitely states that only one hemipenis is inserted at a time while Klingelhöffer refers to the employment of the double penis by the male. Lindholm (1902) also failed to observe any female courting in a subspecies of *L. agilis* but refers to the male as attacking the female and employing peculiar quivering motions with his forelimbs. Since Lindholm describes the inguinal bite and other details as occurring in the same manner as previously reported, he probably witnessed a normal mating.

Klingelhöffer's original observation was based on only six pairs of *L. agilis* placed together in a terrarium. The chief criticism against Klingelhoffer's conclusion that the drumming is intended to attract the males may be taken from his own writing (1900). He once saw a young male carrying out the drumming movements on the approach of another male. Moreover, similar movements are frequently observed in small and presumably immature lizards. No detailed account is given of the effectiveness of the drumming action in attracting the adult male. For the present, then, the question of whether or not the movements of the female really excite the male may be left to future study.

THE BEHAVIOR OF LACERTA VIVIPARA

Other variations in the courtship pattern of *Lacerta* have been reported in *L. vivipara.* In this species the female is larger than the male and it may be seized by the head (Mortensen, 1887). However, the male soon releases his grip and seizes her in the inguinal region. In copulation the male brings his cloaca forward as in other species of the genus. Other variations appear in the length of time that coitus requires in the different species.

THE FEMORAL ORGANS

In no species of *Lacerta* have the males been observed to use their femoral organs as scratching mechanisms. Rollinat (1897) states that in *L. muralis* the femoral organs prevent the slipping of the thigh of the male on the smooth skin of the female at the moment he brings his cloaca forward in contact with that of his partner. Femoral organs are well developed in both *Ameiva* and *Lacerta.* In the former they function to quiet the female, and in the latter they are reported to aid the male in

bringing his cloaca into position. It has been suggested that femoral organs evolved from hypertrophied scales similar to those found in the male of *Sphaerodactylus* (Noble and Klingel, 1932). Unfortunately, the exact function of these scales in that genus has not yet been worked out. It is, therefore, impossible to state what might have been the original function of the organs.

COURTSHIP OF OTHER GENERA OF LACERTIDÆ

It is probable that the courtship pattern of *Lacerta* will be found in other genera of lacertids. Müller (1901) reports that copulation in *Algiroides* proceeds as in *Lacerta*. Minobe (1927) reports *Tachydromus tachydromoides,* however, as courting more in the manner of the iguanids to be described below. Both sexes exhibit rhythmical body movements before copulation. The male seizes the female's neck in his jaws and apparently does not slip back to the inguinal position. The mating of the Asiatic *Eremias intermedia* has been observed at close hand apparently (Zugmayer, 1909) and yet the male has not been described as biting any part of the female's body. How far the mating behavior of *Tachydromus* and *Eremias* actually diverge from that of *Lacerta* will have to await a more complete study of the performance.

DEFENSE OF TERRITORY

One important difference between the mating behavior of *Lacerta* and that of the teiid genera discussed above is that the latter do not fight among themselves. At least we have never witnessed a fight between courting males while this seems to be the usual procedure in *Lacerta*.

In *Lacerta* fighting between the males has been recorded in several species and probably occurs in all. These fights do not always end in injury to the defeated male even in the powerful *L. ocellata* (Tofohr, 1909). Gesticulating and bluffing appears to form a large part of the fight repertoire of all lizards.

The fact that the male *Ameiva* does not fight, and *Cnemidophorus* only rarely during the breeding season may be one of the reasons that these two genera are gregarious or, at least, that large numbers are seen together in certain favorable places. Rollinat (1900) noted that the young of *Lacerta viridis* form aggregations while the adults usually live in separate territories. He observed further that the adults live in particular territories for a large part of the year. Adults of other species of *Lacerta,* it is said, also live in circumscribed territories for part of the year. Wiedemann (1909) states that the adults of *L. oxycephala* leave their winter

quarters in April and settle in new territory, which is usually occupied the whole summer. If a lizard is captured in such a place and escapes, it will be found again close at hand.

The male protects his domain from intruders. Bitter fighting ensues when the males meet. The fights are waged among the rocks, the conquered dashes away, jumping cracks half a meter wide without hesitancy. Suddenly, the pursued may turn on his enemy and, in a second, both lizards are a single moving ball until the conquered one takes again to flight and disappears from the invaded territory. Then the victor returns to court the female that has indifferently watched the struggle.

From the above summary of Wiedemann's account it may be assumed that, once a male has selected a territory, he fights with any other male that chances to trespass on this ground while he courts any female. Sex discrimination is made rapidly and presumably by vision. The reactions toward a male are different from those toward a female. Hilzheimer (1910) has reported an observation he made of *L. agilis* in the field which lends support to this point of view. While walking along a country road in May he saw a female in the embrace of a male attacked by another male. Hilzheimer gives a very detailed account of the fight that ensued. The attacking male was larger than the male embracing the female. Nevertheless, the small male on the back left the female immediately, and the males chased each other in the grass and then ran again in the road. The female continued her journey toward the other side of the road. The large male, after defeating his rival, remained quiet for a while and then ran after the female. After he reached her, he walked a few paces along with her and bit the female suddenly once or twice in the tail about 1 cm. behind the legs but, when the female did not respond, he bit her body and neck. The female did not pay any attention and walked quietly on. Then he mounted on her back and was brushed off by her in the grass. The biting behavior and mounting were repeated several times. Meanwhile the small male, which remained in the place where he had taken refuge, began to move and rushed after the female. When he came near her, the large male was on her back and, when the large male noticed the approach of the small one, he leaped from the female's back toward the rival. They chased each other again in the grass; the small male escaped and this time disappeared in the grass. The male again hurried toward the female, repeating the courting performance.

Although from Hilzheimer's description it might be assumed that males can distinguish sex at a distance and respond according to this recogni-

tion, it is also possible that the male in possession of the female was merely responding to an attack reaction of another lizard with a counter attack. Under such circumstances the bright colors of the breeding male would serve merely to make the fighting lizards more conspicuous to each other. It is, of course, possible that the males had previously engaged in battles and responded at once to the presence of a lizard in male livery with the fight reaction. Since lizards in captivity quickly learn the feeding routine, it is obvious that learning cannot be entirely ruled out of the courtship performance.

IGUANIDÆ

The Iguanidæ and the allied Agamidæ include some of the most extreme types of sexual dichromatism. These two families are included in Iguania, one of the most primitive groups of lizards (Camp, 1923), but they have advanced beyond most families of lizards in the degree of specialization in sexual differences of color. This specialization is presumably correlated with some functional requirement but, as indicated above, there is no agreement as to the nature of this requirement.

ANOLIS UNDER LABORATORY CONDITIONS

We may consider first the mating behavior of *Anolis* since the genus has been more fully discussed than any other group of lizards with the possible exception of *Lacerta*. We have studied five species of *Anolis* under laboratory control. Although the cages were uniform with those employed in all of our observations, the lizards of this genus were fed meal worms and wax worms. *Anolis* is usually kept with success in terraria well provided with growing plants but we found it advisable to use bare branches for perches and to control the humidity by dampening the gravel floor of the cages. Such an arrangement made it possible to follow the movements of individual lizards but few of our *Anolis* lived over a year under these conditions. Most of our observations were made during the first two or three months after shipment from the field.

RECORD OF MATINGS OF ANOLIS

During the period of observation records were made of twenty-one copulations in this genus. One was in *Anolis cybotes,* three in *A. inaguæ,* five in *A. sagrei,* five in *A. porcatus* and seven in *A. carolinensis*. Of these twenty-one matings ten, or nearly half, were instances of males copulating with males, only eight were with proved females, while in three cases the sex was unrecorded. We endeavored to determine sex by a

cloacal examination immediately after copulation but in some cases the mated lizards could not be retrieved with certainty before they were lost among the others in the cage. Sex was also checked by an extension of the throat skin. In all of the above species the males have a far more developed dewlap than the females. All of the species of *Anolis* available copulated with males at least once. So far as we are aware, only Schulz (1931) has previously recorded a male *Anolis* copulating with a male. Our observations, however, indicate that under laboratory conditions homosexual matings are of frequent occurrence. Apparently males have considerable difficulty in distinguishing sex. We have seen no evidence in our series of observations that females of *A. sagrei* can recognize males of their own species at a distance, as Mertens (1926) suggested. The female in all of our observations played a purely passive rôle.

COURTING AND MATING BEHAVIOR OF ANOLIS

Although fighting is nearly a daily occurrence throughout the spring and early summer, we found matings to be decidedly rare. No doubt, they occurred much more frequently than our records would indicate but, as they take place very quickly with very little preliminary movement, they are apt to pass unnoticed by the observer who is watching several cages at one time. A male beginning to court proceeds much in the manner of a male starting a fight but the attitudes are less extreme. He challenges his partner with one or more nods of the head and frequently expands his dewlap. Very rarely, however, will he raise the soft skin along the midline of the neck and back until it forms a low crest similar to that which is usually produced by a fighting male. The preliminary challenge is immediately followed by the male's seizing his mate by the nape of the neck (Fig. 5A). After a moment's hesitation during which the grip is secured more firmly, the courting male begins a violent struggle to force his tail under that of his partner and to bring their cloacas in contact. In doing this he may rub his partner's flank with one of his hind limbs but these rubbing movements are poorly directed and do not form a definite phase in the courtship as they do in *Ameiva*. Femoral organs are lacking in the *Anolis,* and any quieting effect, if it occurs at all, must come from the friction of the thigh skin against the flank. If the mate does not greatly resist the attempt of the male to throw his tail into the position for copulation, the courting male struggles very little and leg rubbing does not occur. The male usually maintains his grip on his partner's neck throughout coition but occasionally, especially if the female
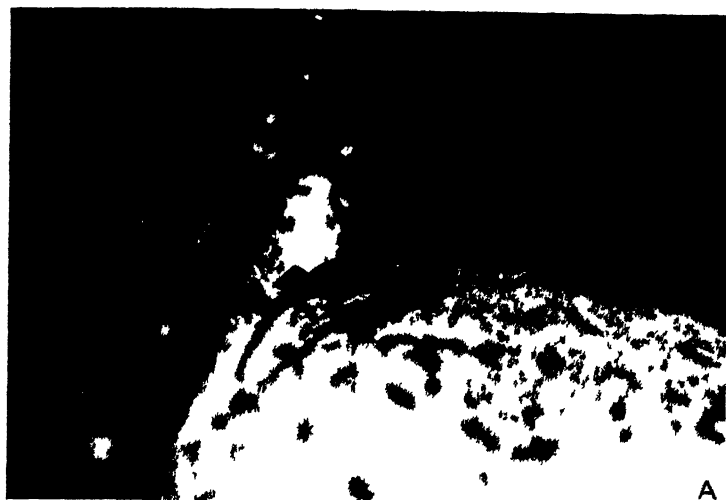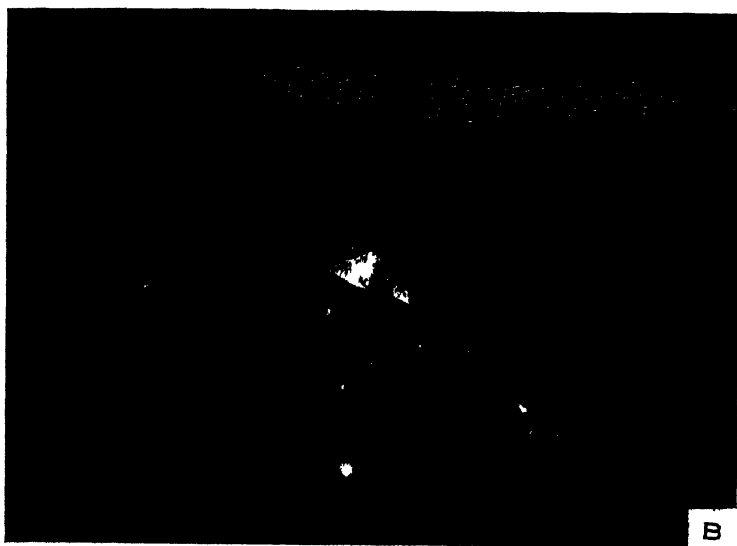
FIGURE 5.—The mating behavior of *Anolis porcatus*.

A.—A large male attempting to secure the usual neck grip on a small female seizes the side of her head in his jaws.

B —A male copulating with another male assumes the normal posture characteristic of the genus.

is small, he may release his grip after his hemipenis has been inserted into the cloaca of his partner.

The courtship and mating pattern is the same in all the species of *Anolis* studied. Specific differences are found chiefly in the length of coition. Four uninterrupted coitions in *A. carolinensis* were approximately 15, 20, 26 and 39 minutes respectively. During one of these the male moved h⁺s cloacal region back and forth in a rhythmical manner for the first two minutes. A similar movement was noted once in the five *A. sagrei* matings. The longest coition in this species lasted eighteen minutes. All coition periods other than those mentioned above lasted between one and five minutes. Some of these short periods were interrupted by the observer but some were apparently voluntarily cut short. Danforth (1925) records an apparently interrupted coition of *A. cristatellus* as lasting three or four minutes. It is interesting that the mating of this species as observed by Danforth in the field is the same as that witnessed by us in the laboratory in the case of other species of the genus. Danforth reports that the male during coition remains perfectly still and allows close approach. Hence, the few cases of movement during coition reported above in other species may not be typical of *Anolis*.

HOMOSEXUAL MATINGS COMPARED WITH NORMAL MATINGS

Although the mating of *Anolis* has been previously described, the frequent occurrence of homosexual matings under laboratory conditions has never been stressed previously. Copulation proceeds in the same manner whether a male selects another male or a female for his mate. Two records from our daily record book may be given to illustrate this point.

Male Mating with Female

July 8, 1930.

A series of *Anolis sagrei* arrived on July 6. Today they began to court. That is, the males instead of merely fighting among themselves attempted to seize less vigorous individuals by the nape of the neck. These seizing movements were, in some cases, preceded by head nodding and throat extension. Two matings between males and females occurred. The male seized the back of the female's neck firmly in his mouth, held her a few seconds, and then endeavored to bring his tail under her tail and his cloaca forward until it was in contact with hers; thereupon one hemipenis, that adjacent to the female, was inserted. One of the two copulations

lasted approximately five minutes. During part of this time the pelvic region was moved forward and backward rhythmically. The interval between the forward thrusts varied from two to eight seconds.

Male Mating with Male

February 20, 1931, 8.25 a.m.   Room temperature 82° F.

A large male of *Anolis carolinensis* began to court a smaller male of the same species. When the small male was seized by the back of the neck, he thrust out his dewlap and struggled about the cage but could not free himself from the grip of the larger male. After four minutes of struggling the seized male became quiet and the larger male thrust his tail under that of the smaller one, the cloacas were brought together and copulation began. It lasted thirty-eight minutes, forty-five seconds. During this protracted period the small male only once endeavored to free himself. Two other males were fighting in the cage and one of them fell on the pair without interrupting their copulation.

AN EXPLANATION OF HOMOSEXUAL MATINGS

This was the longest coition we have recorded in any species and yet it was between two males. Why do courting males confuse males with females? We gained some light on this question by checking up on the males which submitted to copulation. In one case the male was apparently sick. This was definitely so in the case of the *Anolis sagrei* male which submitted to copulation on June 8, 1930. In four of the homosexual matings of *Anolis* a smaller male was seized, and there is one record of a male the same size as the courting male having been forced to play the part of a female (Fig. 5B). In general, but not always, it seemed to be the weaker or smaller males which were forced to function as females.

DOMINANCE

The literature presents no evidence of any homosexual mating having occurred in nature. Males tend to fight and would, no doubt, tend to mark out territories for themselves as has been described in the case of *Lacerta*. Even in the terrarium observers such as Zapf (1911) have reported that one male will dominate all the other males of his own species. In our laboratory we always kept several healthy males and females together in the observation cages and, while fights between the males were of frequent occurrence, only rarely did we observe behavior which could be definitely assigned to dominance. The clearest case may be described

in full.   During three successive days in June. 1932, while experiments were being conducted with courting *Anolis* in one cage, one male that was as large as any in the cage was clearly dominating all the others.   As soon as the room became warm with the heat of the day (i. e., approximately, 80° F.), this one male was seen to be continuously light green, walking up and down the branches in the cage.   Occasionally he would throw out his dewlap, nod, and approach other lizards near him evidently to chase them off or court them.   Usually the other lizards in the cage were brown and had their eyes on the green male, and usually they avoided him when he approached.   At times, however, a male would accept the first male's challenge and the two would flatten their sides, bob and threaten each other in the manner described below.   The second male, during these days, invariably gave way to the first.   The latter rarely courted during these days; he was continuously in the state of great excitement which is followed by fighting, not courtship.

THE METHOD OF FIGHTING OF ANOLIS

The method of fighting of *Anolis* may be described in further detail because it has an important bearing on the genesis of secondary sexual characters.   The male is usually excited by the approach of another lizard. He protrudes his dewlap to its fullest and retracts it again.   In several species the skin along the back of the neck is raised into a fleshy crest, a low ridge is raised along the back and the body is remarkably flattened. The extension of the dewlap may be repeated at intervals of a few seconds. Soon, rising high on all four legs, the male stiffly nods and turns his side toward the possible rival.   Although his legs are straightened, the ventral margin of the compressed belly scarcely clears the ground.   In brief, the male attempts to make himself look as big as possible in the eyes of his rival.   If the male was dark brown or dark green at the beginning of this performance, he will soon turn to a bright green.   The breeding male, in the spreading of his dewlap and the lateral advance toward a rival, presents to him a greater display of color than such a male ever presents to a female or weak male with whom he will mate.

Both the female and the male of *Anolis* when in sunlight or in a warm room will bob their heads at intervals and jump about from one branch to another, and the males will occasionally throw out their dewlaps. Courting males do more bobbing than this and extend the fan more often. Moreover, they will chase other individuals which do not answer the challenge with a similar display.   If fighting continues, the males will fre-

quently spring at the adversaries with open mouths. More often, however, they merely sidle up to them with sides extremely flattened.

A display of color in *Anolis* is, therefore, primarily a bluffing mechanism. Often a rival makes no response but keeps his eye on the display before him and moves off when it comes too close. As we shall see below, this is the "rule of the game" in other iguanid genera. If the rival stands his ground, he will usually spread his throat fan, compress his body and turn sideways toward his opponent. Frequently the fight will end at this point, the male that was most impressed by the display quickly dropping his crest and slinking away. At other times both males open their mouths wide and rush at each other. If they meet head on, the jaws may lock but, when space on the branch is available, they usually move broad side toward each other. In this case an effort is made to seize a limb of the opponent. The display of *Anolis*, although primarily bluff, is not wholly so, and possibly this is one of the reasons why there is not a greater sexual difference in color.

There is, however, one other fact to consider. A lizard on a tree is in a more exposed position than one on the ground. A high premium is presumably placed on protective coloration in the former situation. *Anolis*, by keeping the bright dewlap hidden except at odd intervals, is avoiding the danger of attracting hawks or other enemies.

THE HEAD NOD

It may be noted that the head nod itself is not primarily part of the bluffing mechanism, for it is practiced by females and even by recently hatched young. It is a common reaction in all Iguanidæ and Agamidæ but has not been seen in the lizards of any other family which have passed under our observation. Schmidt (1911) has reported an active head nodding in *Mabuya carinata* but we have not seen it in a large series of *Eumeces obsoletus* and *Leiolopisma laterale* which we have kept in observation cages.

The function of the head nod is not definitely known. It very probably aids vision by permitting several views of the same object from slightly different angles. Since these views are obtained in rapid succession, the images would tend to superimpose and make the objects stand out from the background. As long ago as 1881, Monks recorded that both sexes of *Anolis carolinensis* nodded upon seeing each other. In agamids, also, head nodding is often directed toward the opposite sex (Brandis, 1911) but also occurs in isolated animals. Sachs (1922) suggested that the reaction may be merely an expression of excitement or

possibly an aid to swallowing. We have noted that the nodding of one lizard will often induce another lizard to nod regardless of sex. In *Leiocephalus* we have frequently observed that the nodding of one individual would induce all the other individuals in the cage to nod. Head nodding, whether or not it aids vision, is obviously a group response. It may serve to place all the lizards in a restricted locality on the alert at the approach of an enemy. We have never seen a lizard nod when its eyes were closed. In gregarious species this mutual stimulation would tend to induce the individuals in any one locality to respond as a group.

FIELD OBSERVATIONS ON ANOLIS CAROLINENSIS

Although the mating of *Anolis* as observed in the laboratory proceeds the same as that recorded by Danforth in the field, there is probably one very fundamental difference. In the field the individuals are far more scattered than in the laboratory. Where fights have been observed, they were always between isolated pairs. Mr. Morrow J. Allen, while carrying on field work for the American Museum near Biloxi, Mississippi, witnessed one such fight between two males of *A. carolinensis,* on April 2, and another between a different pair the following day. We quote from Mr. Allen's field notes:—

10.40 a.m. The two males were about twelve feet from the ground on the upper surface of a tree trunk and circling slowly about each other while maintaining a distance of ten inches apart. Their bodies were compressed and they walked slowly and stiff-legged with bellies raised from the surface. Their throat fans were extended frequently but seemed to be correlated with no other movement except that of bobbing up and down. A low crest was raised along the neck. One of the lizards was the larger but as the pair closed in combat, now one and now the other, would take the aggressive. They circled for a few minutes and then the larger walked stiffly for a few inches up the tree, the smaller following. The larger turned and bobbed. The second advanced. The mouths opened and the pair began to spar with their jaws, making audible crunching sounds at each bite. Soon the jaws locked, the smaller lizard had the snout of the larger one firmly clamped. They remained with locked jaws for approximately two minutes when they separated and remained for a moment staring at each other.

The larger then continued his progress up the tree with the smaller lizard following to one side and slightly behind. Again the first turned, once more sparring with the jaws, and the jaws locked exactly as before. The lizards remained in this position for about one minute; then they began to twist their bodies. The latter movement caused them to fall from the tree to the upper branches of a bush six feet below. The larger lizard hung by its hind feet from a small limb, the smaller one supported itself only by the locked jaws. Five minutes elapsed before they separated, the smaller lizard falling to a

branch a few inches below, the larger one drawing himself up to the branch on which he had caught.

The two combatants eyed each other for a moment and then each began to move toward the main vertical branch of the bush, proceeding on stiff legs with compressed bodies. They reached the main stem simultaneously and continued to draw near. Again sparring began and the jaws locked. This time the position was maintained for approximately eight minutes. Separation was accomplished by head-shaking. The smaller lizard climbed out on a small branch that grew close to the trunk of the tree they had fallen from. He jumped the intervening space and traveled up the trunk of the large tree in a leisurely manner. The larger one followed about five minutes later after looking directly at the observer. The lizards were observed through the field glasses as they met high up in the tree. Again they circled slowly, but intervening leaves prevented a clear view of the procedure. Eventually they were lost to sight.

Fifteen or twenty minutes later the struggling pair dropped from a height of twenty feet to a bush below. This time the larger one had a firm grip on the head of the smaller one. His upper jaw was holding directly behind the eye of his opponent while his lower jaw was across his rival's throat. The lizards were suspended by the hind feet of the larger male. After five or six minutes a sudden wriggle freed the smaller one, which fell several inches to another branch. With neck crest raised and dewlap partly extended the small male began to retreat through the bushes. Soon the crest dropped, the throat fan was retracted and the conquered male worked his way to the ground. This struggle, in which first the smaller and then the larger male had the advantage, lasted approximately one hour and forty minutes.

If it had been a female which had come into the tree occupied by one of the males, no fight would have occurred because female *Anolis* according to our observations do not fight. To judge from our laboratory observations we may assume that the male, after challenging the newcomer with an extension of his dewlap and receiving no answering challenge, would swing directly into his courtship pattern. He would endeavor to grip the newcomer's neck. In the crowded conditions of the laboratory we may assume that many attacked males do not have time to call forth by a flourish of the dewlap the fight reaction of a male intent on mating. If the courting behavior is not checked in this manner, the attacking male continues until he has actually copulated with the male. The structure of the male's cloaca permits such homosexual unions and the sperm which is found there after mating is, in all probability, deposited by the attacking male. It follows from this interpretation of the mating reactions in *Anolis* that the bright colors of the male dewlap have evolved as frightening devices, and not at all to stimulate the female to mate. We shall present evidence that this is true for other genera of iguanids as well.

THE FIGHTING OF LEIOCEPHALUS IS LARGELY BLUFF

Of the lizards which we have studied in the laboratory, the species of the genus *Leiocephalus* exhibited the most extreme stages of sexual dimorphism. In this genus, perhaps more than in any other, the bright colors of the male are clearly used as bluffing mechanisms. As in *Anolis*, the fighting reactions may be distinguished from the courting reactions although they have certain elements in common. Again as in *Anolis*,
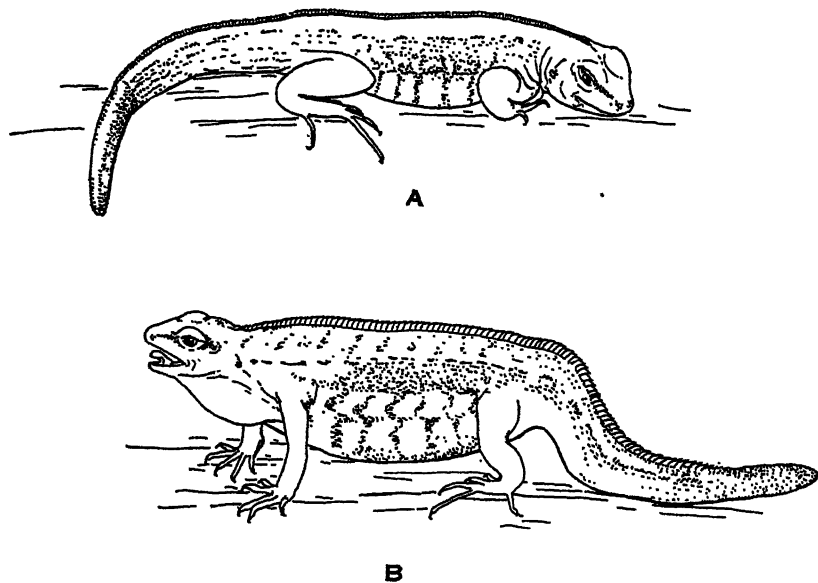
FIGURE 6.—The bluffing pose of the male *Leiocephalus schreibersii*.

A.—In the resting position the transverse bars of pink and blue are scarcely visible.

B.—In the bluffing attitude the body is compressed, the throat extended into a small dewlap, the dorsal crest erected and the tongue thrust out of the mouth. The bluffing lizard moves laterally towards an opponent displaying his bright flanks to the fullest.

the most extreme displays of color are directed toward rivals and not toward possible mates.

In the laboratory the male *Leiocephalus* frequently fight among themselves. We have studied *L. schreibersii* and *L. inaguæ* in large series, and a few *L. personatus*. Two males will simultaneously rise on their legs, turn their sides toward each other, raise the ridge along their backs and flatten their throats to form feeble fans or dewlaps (Fig. 6). At the same time they flatten their bodies vertically until, viewed laterally, they appear very large and very brilliantly colored. Viewed either

FIGURE 7 —Success and failure in bluffing

A —*Leiocephalus schreibersi* in bluffing pose keeps a rival at bay
B —A male *Sceloporus undulatus* seized by two other males who are intent on mating

caudally or cephalically, however, they look knife-like in their flatness. Although they stand high on their legs, the sharp lower line of the belly nearly touches the ground. They then attempt to bob, in a stiff manner, their whole body rocking back and forth in a fore and aft direction. They move around, always keeping their flattened side toward the opponent, at the same time that an eye is kept on him (Fig. 7A). Often, at this stage, one or the other lessens his display, and is bluffed into a cowering position, whereupon the fight is over.

When neither will lessen his display, the combatants become more aggressive, thrusting their tongues well out of their mouths and quivering all over. A moment later one will dash up to nip his rival in the ear region. The second one jumps away, exposing first one broad side and then the other while attempting to nip back. They rarely catch hold and, even when they do, never injure each other. This is the more remarkable in that *Leiocephalus* is a voracious feeder, being known to have killed and devoured full grown *Ameiva* (Noble and Klingel, 1932). A *Leiocephalus* fight is purely a magnificent piece of bluffing.

More than two may take part in the demonstration but this is so confusing that the fight does not last long. A male never fights a female. However, on three occasions (two of *schreibersii* and one of *inaguæ*) females have been seen fighting each other. They attempted to do the same thing males do, even to thrusting out their tongues and nipping each other, but they have less dewlap, no fleshy dorsal ridge and no bright colors. These three cases are the only observations we have made of females of any genus fighting. After the most fierce fight, one of the fighting lizards, believed to be a female, was opened and found to have well-developed ovaries. Fighting is not to be confused with the head nodding characteristic of all iguanids and practiced by both sexes and by juveniles. As pointed out above this serves to stimulate the attention of all lizards in the immediate vicinity but it plays no essential part in either the fighting or courting behavior of *Leiocephalus*.

COURTSHIP BEHAVIOR OF LEIOCEPHALUS

The courtship behavior of the three species of *Leiocephalus* is essentially alike. Both courtship and coition are very short. It is usually preceded by a feeble display of color but, so far as our observations go, never by the extreme compression of the body and grotesque "rocking horse" movements of the fighting males. With very little preliminary, the male rushes forward and seizes his intended mate by the back of the neck. Often the male lets go and seizes his mate's neck again several times in

succession. During this period the male remains erect on straightened legs, with compressed body showing off the bright tones on the sides of his body to advantage. However, he is usually standing slightly caudal to the female and in such a position that she can see very little of this display. The female does not show any response to this treatment other than an occasional effort to escape. Frequently, the male maintains his grip once he has grasped in his jaws the thick skin on the back of the female's neck.

Fifteen *Leiocephalus* matings were recorded. In only one of these the male was seen to rub his cloaca from side to side on the ground like an *Ameiva* beginning to court. In three matings the male bobbed his head up and down after he had grasped his mate. Although no femoral organs occur on the ventral surfaces of the thigh of the male, most of the males, once they had secured a firm grip, began to rub one of their thighs along the back of the female in nearly the same definite manner found in the teiids discussed above. The whole mating procedure is run through so much more quickly than in the Teiidæ that this rubbing appears to form only a small part of the courtship of *Leiocephalus*. During the rubbing the male thrusts his tail under that of his mate and brings their cloacas together. The grip on the female's neck is maintained throughout coition which is very short. The longest recorded courtship in the genus was five minutes, the longest coition forty-five seconds. In the length of coition there is a striking difference between *Anolis* and *Leiocephalus*.

The fifteen matings we observed are, perhaps, too few to distinguish specific differences in the performance. In two cases of *L. schreibersii* matings the males were observed to thrust the pelvis forward in a rhythmical manner. This movement differed from the similar behavior in *Cnemidophorus* in that the first thrust served to insert the partly everted hemipenis and since the whole coition only lasted from five to six seconds there were very few forward thrusts. The coition also differed from that of *Cnemidophorus* and of most lizards in that the male released the female and withdrew his hemipenis while it was still everted.

OBSERVED HOMOSEXUAL UNIONS A RARITY IN LEIOCEPHALUS

Apparently in correlation with the elaborate bluffing mechanism of *Leiocephalus,* we observed only one case of a male copulating with another male in this genus. Of the fifteen copulations recorded eight were in *L. schreibersii* and seven in *L. inaguæ; L. personatus* courted but did not mate. The one instance of a homosexual mating was in *L. inaguæ*.

However, among the thirteen courtships which did not end in coition, eight were with other males. This fact suggests that, while males cannot distinguish males who do not fight back from females, the seized male may not be as passive as a female or, at least, in some way obstructs coition. An adult female of the species under consideration is usually smaller than an adult male but size does not play an important part in the initial phases of courtship for we have seen adult males courting other males as large as themselves.

THE BEHAVIOR OF THE FEMALE

During two courtships, one in *L. schreibersii* and another in *L. inaguæ*, the female appeared to take an active part. When a female is approached by a courting male, she usually attempts to avoid being bitten by making a hasty retreat. Once the male has secured his grip on her neck, the female no longer struggles. In the two cases under consideration the male attempted to bite the neck of a female, but in each case she moved away and turned her tail and posterior part of her body toward him. Rising high on her hind legs, but keeping her chest low, the female swayed from side to side. Such a position would presumably facilitate the male's thrusting his tail under that of the female. In each case a second male interfered, threatening to fight, and the courting behavior terminated. Taken by itself, this behavior on the part of the female *Leiocephalus* might be considered an invitation to mate. However, in another iguanid genus *Sceloporus*, a somewhat similar behavior forms a normal part of the daily activity of one species at least. A discussion of the significance of this behavior may be reserved until the data concerning *Sceloporus* is before us.

The mating behavior of one pair of *Leiocephalus* in a cage frequently stimulated other lizards in the cage into activity. This is one of the reasons that more courtships did not end in coition. In two courtships completion of the mating was obviously prevented merely because another male compressed his body into the usual bluffing attitude. Three others were discontinued by the actions of a second male, who bit the female's tail, causing her to jump so violently that the courting male lost his grip on her neck. Once a rival male actually bit off the end of a female's tail.

RECORD OF OBSERVATION

In concluding this outline of the mating of *Leiocephalus*, the record of a typical mating may be quoted from our record book.

A Typical Mating of Leiocephalus schreibersii

June 4, 1929.   Room temperature, approximately 80° F.

A male *Leiocephalus schreibersii* attempted to mate with a female of the same species.   She did not resist.   He seized her by the back of the neck and stood over her for a moment.   Then he began to move his pelvic region from side to side for a few seconds.   A moment later he began to rub his leg along the side opposite to that on which he later stood.   This rubbing gave the impression that the male was merely attempting to brace himself by pushing backward with his hind leg.   He held the female's neck firmly during these movements but, before he could bring their cloacas together, the female jerked away.   Fifteen minutes later the same male seized the same female again and engaged in the same pelvic and limb movements as before.   This time the limb rubbing resembled closely that of *Ameiva*.   The neck grip was maintained except when the male was trying to improve his hold.   By moving his hind limbs the male brought his cloaca in contact with that of the female.   Then he began to move his pelvic region forward in little spasmodic thrusts.   Five seconds later the hemipenis was withdrawn.   It was fully extended and remained so for approximately three seconds.   The male then dragged his cloaca on the ground for a few seconds as his excitement faded away.   The female made no resistance throughout the procedure and did not run away after being released by the male.

In spite of the few cases of female fighting reported above, it may be emphasized again that the female *Leiocephalus* shows no evidence of being stimulated by the color or attitude of the male.   A single case from the daily record will serve to show how most courtships begin.

Preliminaries of Courtship

April 10, 1931, 9.30 a.m.   Room temperature, approximately 84° F.

A male *Leiocephalus inaguæ* was seen moving his left thigh back and forth in a nervous fashion.   He looked around the cage and approached three females, biting each one in turn on the neck without maintaining a firm grip on any one.   At the moment of biting the male moved his pelvic region from side to side and vibrated his tail slightly.

SCELOPORUS

The third genus of iguanids which we have studied in the laboratory is *Sceloporus*.   Although this genus includes the well-known fence lizards, the mating behavior has never been completely described in any form.   We

had two pairs of *S. magister* which courted without copulating. We had a large series of *Sceloporus undulatus* courting and fighting. We shall limit our discussion to the behavior of this species.

THE POSTURE ASSUMED BY THE FEMALE OF SCELOPORUS

Sceloporus differs from all the other genera studied in that the females as well as the males have their own sexual activity. There is, as in *Anolis* and *Leiocephalus,* the ordinary quick head bobbing by both sexes, expressive of alertness. Besides this, the males have a "sex bob" (Fig. 8C). It consists of slightly flattening the sides, making the gorgeous blue bands fully visible, followed by a raising and lowering of the body in which the front legs only are used. Apparently this does not stimulate females in the least, and may or may not be followed by courtship. Females also have a definite posture, which is peculiar to their sex. It consists of rising high on their four legs and hunching the back until it forms a dome (Fig. 8B). No male was ever observed to assume this attitude. Sometimes the female holds this position indefinitely, but usually she hops up and down on the ground in a stiff-legged fashion, progressing forward about two centimeters with each hop. This performance never seems to stimulate males. It is, however, often provoked by the nearness of a passing male or by an attempt at courtship, but may occur when no males are active. We could secure no evidence that this indicated a willingness on the part of the female to mate. It has nothing to do with ovulation, for eggs were not found in the oviducts of one "hopping" female which was dissected.

COURTSHIP AND MATING OF SCELOPORUS UNDULATUS

Sceloporus males court very often but copulation rarely occurs, due apparently to the resistance of the female. After holding a female's neck and bobbing, the male begins to try to place his tail beneath hers and to bring their cloacas together. Sometimes this is accompanied by leg rubbing, as in *Ameiva.* Even though *Sceloporus* has small but well formed femoral organs, leg rubbing is rarer in this group than in *Leiocephalus,* which lacks femoral organs entirely. Copulation may occur at this point in the courtship and it is extremely short, lasting only a few seconds. The hemipenis is usually visible after coition is completed. The neck skin of the female is usually held throughout the courtship and through coition if one occurs.

Only four copulations followed courtship in our series of *S. undula-*

tus, and in each case the mate was a female. Also, in each case there was no leg rubbing, and in three cases the male held the female's neck skin until coition was over. Coition itself lasted only two or three seconds. Thirty courtships which proceeded as far as neck biting were re-
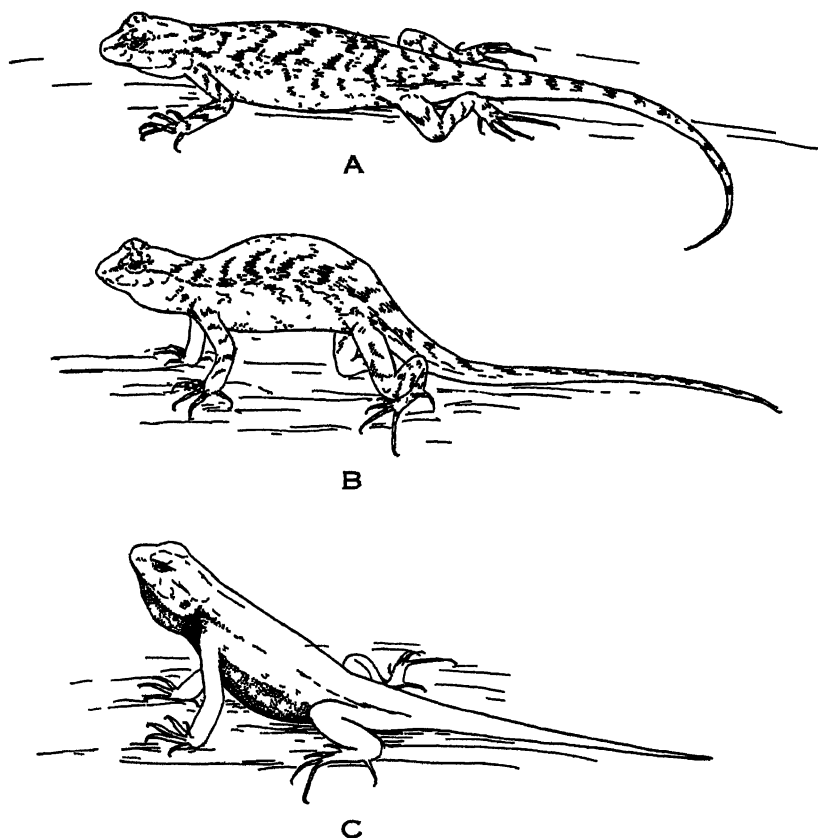
FIGURE 8 —Three poses of *Sceloporus undulatus*

A.—Female at rest.

B.—Female in hunched or "dome" pose

C.—Male giving the "sex bob." Only the forelegs are straightened when the male is displaying before a female. All four limbs raise the body from the ground when the male is threatening a rival.

corded. Thirteen of the thirty were with females, eleven were with males and six were uncertain as to the sex of the mate. There is such a marked difference in color between the sexes that sex may be identified without cloacal examination. In the doubtful cases mentioned above, the seized lizard escaped before it could be examined.

It would seem, then, that in spite of the marked difference in color and posture of the sexes, the opposite sexes neither excite nor attract each other. A male intent on mating is unable to distinguish a quiet male from a female (Fig. 9). We shall see below that this conclusion is not fully borne out by observations in the field although it appears to hold for our laboratory material.

COURTSHIP BETWEEN MEMBERS OF DIFFERENT SPECIES

We rarely have kept different species of *Sceloporus* together in cages, but Speck (1924) has recorded a courtship between a male *S. undulatus* and a female *S. spinosus*. Grijs (1899) observed a *Sceloporus undulatus* courting an *Agama mossambica* and an *A. stellio*. The courtship progressed only so far as the neck hold. Since sex recognition, according to our observation, is due to a failure to fight, crossing of compatible species should not be difficult.

OBSERVATIONS ON NORMAL AND ABNORMAL MATINGS

Hyde (1923) has witnessed portions of the mating behavior in a single pair of *Sceloporus undulatus*. Since this is the only previous description of the mating of one of the commonest lizards in eastern United States, it is unfortunate that Hyde witnessed an abnormal mating. He reports seeing a male bite a female several times in the side of the neck. Fifteen minutes later he observed the pair with ventral surface adpressed, and the male with one hemipenis inserted into the female's cloaca.

On six different occasions we have noted females, when seized by the neck, tumbling over on their backs in their effort to escape. In every case, however, the male forced his tail under that of the female, endeavoring to bring his cloaca to the position where the female's cloaca would have been if she had not rolled over. As soon as his cloaca reached this position without attaining the expected contact, the male released his grip. In no case was a hemipenis inserted into the female's cloaca while their ventral surfaces were in broad contact. Hence, it seems highly probable that the female observed by Hyde turned over after coition had begun. The wriggling described by him is not part of the normal mating procedure in the fence lizard.

As in *Leiocephalus*, the courting of one lizard may stimulate other lizards in the cage. In four of the thirty courtships mentioned above, a rival male seriously interfered with the progress of a courtship (Fig.

FIGURE 9.—A failure of the mechanism of sex discrimination. The male at the top of the piece of bark is attempting to mate with another male who is defending himself with one hind leg. In the meantime two females (with mottled backs) are passed unnoticed by the courting male. Male *Sceloporus*, like other male lizards, are unable to distinguish passive members of their own sex from females.

7B). In one of the cases the rival male merely compressed his body and bobbed his head in the manner of a fighting *Sceloporus*. In three other cases the rival nipped at the courting male's tail, causing him to turn and assume the usual fight attitude.

FIGHT REACTION OF SCELOPORUS UNDULATUS

The fight reaction of *S. undulatus* resembles that of *Leiocephalus* but is less extreme. The male compresses his body with the result that the blue stripes on the ventral part of the sides are brought into full view. The skin in the midline of the back is raised into a low ridge which increases the apparent height of the lizard. Rising stiffly on all four legs the male turns broadside toward his rival as if he intended to impress him with both his apparent size and splendor. Then, still keeping his bright side toward the rival, the aggressive male bobs up and down on all four legs. If this fails to put the rival to flight, the aggressor will frequently rush forward and bite the other lizard in the tail. The attack of *S. undulatus* is apparently usually aimed at the tail, while in other iguanids, such as *Leiocephalus* other parts of the enemy are also seized. Females, according to our observations, never fight and this fact appears to form the basis for sex recognition. They may, however, resist with their teeth the attack of a male, and this is especially true of females in the field.

It should be noted that the fight behavior differs fundamentally from the courting behavior even though the two kinds of response may follow one another closely. In this connection we may quote from our daily record a case where a courting male was forced to fight but soon returned again to court.

Alternation of Courting and Fighting

April 10, 1929, 3 p.m.   Temperature 79° F.

Several female *Sceloporus undulatus* were under observation together in a cage. One female had her back hunched in the peculiar dome manner when a male began to court. He bobbed up and down utilizing his front legs only, and dashed toward a female, but not the hunched one, and seized the side of her body with his jaws. Both lizards bobbed, the female with her front legs, the male with only his hind legs, because the forepart of his body was held down by his grip on the female. Another male dashed forward and bit the first male in the tail. For a few seconds the first male maintained his grip and then, while rapidly bobbing, he turned and assumed the fighting pose. His body was now compressed and he raised high on all fours, displaying himself to far better advantage than when he had been courting. The second male fled at this show of color and size. The first male, still bobbing, changed from the "fight bob" to the "courting bob." His sides became less compressed, the hind legs were employed less and less until finally only the forelimbs were

brought into play at each bob. The male was now in his original court-
ing pose and, turning back to the female, he caught her firmly by the
neck. Again he bobbed and the end of his tail vibrated. For five or
six seconds the pair remained quiet and then the male brought his cloaca
in contact with that of the female. Copulation lasted scarcely more than
a second. There were no leg rubbing nor trembling movements. The
hemipenis remained extended for a fraction of a second after it was with-
drawn.

MATING BEHAVIOR OF SCELOPORUS SPINOSUS FLORIDANUS

Newman and Patterson (1909) have made a very comprehensive study
of *Sceloporus spinosus floridanus,* a close relative of the eastern fence
lizard, but their conclusions as to mating behavior of this species are
totally at variance with our own. They state:

> The male is apparently the aggressor in seeking a mate, although the female
> undoubtedly exerts a considerable influence on his choice. Observations show
> that she performs certain movements that serve to attract the male from an
> adjoining tree as much as thirty feet distant; and there is no doubt that she
> is more highly excited sexually than the male.

Newman and Patterson do not describe these movements of the female
nor do they give any details as to exactly how a male is attracted by a
female. In *S. undulatus* the only distinctive movements of the female
are associated with the hunching and hopping behavior. We have failed
to find that these movements either attract or stimulate the male. New-
man and Patterson describe the male *S. spinosus floridanus* as giving his
greatest exhibition of color in the presence of the female. After that the
pair slowly circle around each other "often as much as three times. The
female then assumes a receptive attitude, is seized readily by the male,
and copulation follows, lasting for about 15 minutes." The writers
then conclude:

> The displaying of the brilliant blue patches at the sides of the neck and
> body is to be looked upon as part of the means by which the male entices and
> thus influences his mate, although we have no conclusive evidence to show
> that such a display of color is of any particular advantage to the male in
> securing a mate.

Apparently all the observations of Newman and Patterson were made
in the field, for they do not describe any laboratory studies. They do not
state how many courtships they witnessed. It seems highly important
that observations on the courtship of *S. spinosus floridanus* be checked
under laboratory control. It is often extremely difficult to be sure of the

sex of two courting lizards unless they can be picked up and examined from the ventral surface. The observer is apt to assume that a lizard which submits to copulation is a female but our observations have shown conclusively that this is not necessarily true.

Newman and Patterson have given, however, a very full account of the relation of *S. spinosus floridanus* to particular home trees. Apparently the species lives in pairs during most of the year. Breeding occurs in the latter part of March. They state:

At that time one may see the male passing from tree to tree, apparently in search of a mate. A male and a female that have been associated in some advantageous retreat throughout the winter months do not necessarily retain their affiliations, but on the approach of the breeding season, they may separate and each choose another individual for a mate. This was especially noticeable in one case where we had observed a male and female together in or near a hollow tree from time to time during the entire winter. When the breeding time came, however, they separated, and the male was observed to be alone for several succeeding days, passing among the various mesquite trees in the immediate vicinity of the home tree. Finally his efforts were rewarded, and he was seen to be mated with another female.

FIELD OBSERVATIONS ON SCELOPORUS UNDULATUS

No detailed information is available on the relation of *S. undulatus* to particular territories, nor in our experience has any large number been captured in pairs. If, however, the males wander during the breeding season, our laboratory observations suggest that they would fight with any other lizard of their own species they chanced to meet. If the attacked lizard failed to respond with a fighting response, the aggressor would soon replace his fighting by a courting behavior. In *S. undulatus* our observations indicate that sex recognition is accomplished merely by the type of response to the aggressive actions of the male.

In the spring of 1933 after the above account had been presented for publication Noble, Hassler and Lipsey attempted to confirm this conclusion by studying *S. undulatus* in the field. By marking individual lizards with numbered skin clips and with small daubs of color they established the fact that many males are found day after day within ranges which may be called their territories. There is, however, considerable overlapping of these territories, which are not nearly so well defined as in passerine birds. A dead male tied to a thread on the end of a pole and dragged before an aggressive male in such a way that his bright ventral colors did not show was immediately seized and copulation followed. Similarly a living male having his legs tied together, concealing his bright colors,

was seized in the normal mating manner and the free male's hemipenis thrust into the captive one's cloaca. These experiments, which will be reported upon in greater detail elsewhere, fully confirm the thesis expressed above that a male that does not show his colors cannot be distinguished from a female.

Noble, Hassler and Lipsey have also compared the reactions of male lizards in the field to males and females dropped quietly into their territories by means of the fishing poles mentioned above. Other females were colored to resemble males with the result that the attack and not the courtship response was evoked. In the field as in the laboratory the full display is given primarily during the fight and rarely, if ever, during a courtship. Although several matings in the field were studied at close range, no evidence was found of a male's enticing a female by a display of color in the manner Newman and Patterson have suggested.

It may be noted, however, that mating in the field is less stereotyped than in the laboratory. The attack of a male may be directed toward any part of his opponent's anatomy. The copulation postures are the same in the laboratory and in the field but the hemipenis is retained within the female's cloaca for much longer periods in the latter situation. Many males in the field retain their hold on the female's neck until they have copulated twice with the same individual. The degree of response varies with the season. Some males at the close of the season, at least, are able to distinguish quiescent males from females.

THE NECK GRIP AND OTHER ATTITUDES OF MALE IGUANIDS

In the above description of the mating of three iguanid genera it has been pointed out that the male invariably seizes the female by the skin of the neck before attempting copulation. In a few cases the male in attempting to secure this hold has seized other parts of the female's body but invariably before the cloacas were brought together the male shifted his grip to the neck hold. It is probable that all iguanids make some attempt to seize the neck of the female during courtship. The neck grip in its typical form is taken by the male of *Chalarodon madagascariensis* (Petit, 1928), one of the few Old World iguanids. *Basiliscus vittatus* seizes the female by the neck but apparently this grip is sometimes not taken in the related *Basiliscus americanus* (Schmidt, 1914). There is one record of *B. vittatus* having held the female by the base of her occipital comb during coitus. Schmidt (1931) reports that males of this species fight furiously for the possession of the female. In another

paper Schmidt (1931a) claims that the males of *Tropidurus hispidus* cannot be kept together in the same cage because they will fight until the stronger kills the weaker.

COURTSHIP OF HORNED TOADS

Only in the horned toads, *Phrynosoma,* does the published evidence suggest that there may be a divergence from the courtship of other iguanid lizards. Edwards (1896) described *P. cornutum* as gripping the female with all four feet and Cahn (1926) describes the male as assuming "a dorsal position above the female much as in the *Anura,* but amplexus is not nearly as violent or does the reflex persist." It is possible that the flattened body of *Phrynosoma* has conditioned the genesis of a modification in the usual iguanid mating behavior. However, the mating of only one species of *Phrynosoma* is known and even this is not known in great detail. Givler (1922) points out that the males of *P. cornutum* appear from hibernation before the females and are present in great numbers on the breeding grounds. Edwards (op. cit.) mentions only the males as quivering with sexual excitement, and it is possible that this quivering response may function in sex recognition the same way as the fight reaction in other iguanids: individuals that quiver or fight not calling forth the courtship behavior of the aggressive male.

BEHAVIOR OF IGUANA

Turning to the opposite extreme of iguanid evolution from the horned toads, namely, to the large iguanas, the known facts of their courtship lend strong support to the thesis advocated above. Peracca (1891) has studied *Iguana tuberculata* in captivity. The males have a type of bluffing display which differs from the display of most iguanids in that the lungs are filled with air to increase the body size and the round forehead is directed in a butting attitude toward the opponent. The males attack each other, using teeth and claws effectively and apparently also the tail. The female is fertilized by the strongest male, which remains master of the camp, forcing all others to flight. Peracca describes the male *Iguana* as seeking out and copulating with two *Amphibolurus,* members of a different family of lizards. Peracca convinced himself that there was absolutely no sexual choice on the part of the female. He cites a case where a female, placed in the presence of three males, was fertilized eleven times without showing the least sign of defense. Neither of the two females described by Peracca fought but passively accepted copulation with males both smaller or larger than herself.

On the other hand, Peracca's males copulated more with one female than with the other. Peracca believed that this indicated that the males chose between possible mates. There was a marked difference in color between Peracca's two females and it is possible that his males had learned to associate copulation with a particular one. In no other lizard has any instance of selection by the male been described.

BREEDING SEASONS

Peracca found that a female *Iguana* would escape from the advances of the male in December. He assumed that females submitted willingly to copulation at particular seasons, while the males were ready to breed at all times of the year. In lizards, such as *Lacerta,* living in northern regions, there is well known to be a definite breeding season during which both sexes become sexually active. Peracca did not observe that a female gives any evidence of choosing between possible mates, and hence the mechanism of sex discrimination probably is the same in *Iguana* as in the other genera discussed above even though their breeding seasons may differ in length.

FEMALE DISPLAY

One observation of Peracca on his series of *Iguana* seems to have an important bearing on our conclusions as outlined above. One of his females beat the ground with her forefeet and attempted to bite the neck of the male. This was the female which seemed to be less attractive to the males, and Peracca interpreted the movement as an attempt to attract the attention of the male. It will be recalled that Klingelhöffer considered a similar movement of the forefeet in the female *Lacerta* an attempt to arouse the male. Mating in *Iguana* occurred most often with a female which did not practice these movements and most species of *Lacerta* mate successfully without recourse to these "signals." Any movement is apt to attract the attention of other lizards but it does not appear that tapping movements form an essential part of the courtship of any species.

A very different type of female display has been reported in *Chalarodon madagascariensis.* The males display with swollen throats and erected dorsal crest very much as in *Leiocephalus.* Further, the rivals place themselves broadside to one another obviously to bluff in the manner of other iguanids. However, the females are reported (Petit, 1928) to run "exhibiting their cloacas to the following males. If the males approach, they stop, supported on their forelimbs; they pull up their hind

legs and remain motionless with tail curled forward" (translation). There is much in this description which is suggestive of the hunch posture of the female of *Sceloporus undulatus,* but Petit does not speak of the posture as optional in *Chalarodon.* Here is a case where a laboratory check on the field observations would have yielded interesting results. With the data available we can neither affirm nor deny that this posture may aid sex recognition. However, it may be assumed from Petit's account that color is primarily used in *Chalarodon* to bluff males and not to attract females.

AGAMIDÆ

PUBLISHED OBSERVATIONS ON VARIOUS SPECIES

We have had no opportunity to make original observations on this family of lizards although many species in the group exhibit bizarre forms of sexual dichromatism well worthy of study. The family is allied to the Iguanidæ and it is interesting to find that all species, so far as known, employ the neck bite as a method of holding the female. Both Annandale (1900) and Smith (1915) have described the male in the field as advancing toward the female, bowing and nodding. The latter observer describes the female as responding to this nodding performance but, as we have stated above, head nodding is not limited to courtship in any agamid or iguanid. Annandale found that when a male is killed while displaying, his place is soon taken by another. This strongly suggests that each male dominates a particular territory. Grijs (1901) observed that males of the same species fought continuously in the terrarium and could not be maintained together. Annandale (op. cit.) speaks of the bright colors in another agamid lizard as "primarily a sexual attraction." Very recently Mertens (1931) has observed the brilliant flying dragon, *Draco volans reticulatus,* in the field and has noted that the male frequently expands his yellow dewlap. Mertens, like many previous writers, states that these movements are produced with the definite intention of attracting a female. As we have pointed out above, no proof of this contention has ever been presented. On the other hand, our laboratory observations on the Iguanidæ clearly show that the greatest displays are used to bluff possible rivals. We may, therefore, assume that the bright colors of the male *Calotes* and *Draco* serve primarily as bluffing devices which, in the first genus at least, aid the males in maintaining definite territories.

Annandale (op. cit.) credits the Malays with the opinion that the agamid *Liolepis bellii* is monogamous and adds that adults are often

taken in pairs. Newman and Patterson (op. cit.) found that the *Sceloporus floridanus spinosus,* although living in pairs during most of the year, changed territory and mates in the spring. It is, of course, possible that the instinct to hold to one territory would be sufficiently strong to keep a pair together for a more extended period. As a matter of fact this appears to be true of *Zonurus cataphractus* as described by Peers (1930). This species lives in isolated pairs in rock crevices. Peers frequently found several generations of young in a single crevice with the parents. Never was there more than a single pair of adults in one retreat. It is interesting that this species, which shows a closer approach to monogamy than any other known lizard, has very little sexual difference in color. Peers describes the male as holding his head in such a way that his bright chin would be visible to the female but this modest display does not compare with that of many agamids that are not known to live in pairs.

COURTSHIP BEHAVIOR OF AGAMA COLONORUM

The common African lizard, *Agama colonorum,* is presumably closely related to *Calotes versicolor* and yet its courtship activities are apparently distinctive. The species, as reported by Lamborn (1913), is apparently gregarious in the sense that several females live within the territory of a single male. Lamborn did not mark the lizards which he found in these territories but he gives his "opinion that these females look to one lord and master only and that every such family is to be found day after day in one particular locality." He describes certain adults coming back nightly to particular sleeping places but adds: "The young lizards wander to a far greater extent, not attaching themselves to any particular group." Although such a "harem" system might develop in any group of vertebrates in which the males dominate particular territories, Lamborn goes farther and credits the females with endeavoring to attract the males. He states:

> The male's responsibilities seem to be in excess of his capacities, so that the females are forced to resort to various artifices to secure their share of his attentions. This solicitation usually takes the form of running up to the male, elevating the tail in front of him and turning it to one side, but even then he frequently responds by biting the importunate female. If she runs away, however, he will sometimes pursue, and unless she allows herself to be caught too readily, her end may be attained. I am sure that this little manœuvre does act as an incentive to the male.

Lamborn does not state how many times he has observed the manœuvre. Many lizards raise the tail and turn it to one side in non-sexual situations.

Until more details are forthcoming we may assume that Lamborn has not proved his case. Other species of lizards have been reported to employ attracting devices but, as stated above, the evidence on which these assumptions were made is very limited.

On the other hand, the published accounts of courtship when given in great detail usually contain some reference to the bright colors as frightening devices. For example, Kinghorn (1931) describes a mating *Amphibolurus barbatus* which rushed at him, at the same time giving a great show of color. The female, which lay prostrate on the ground, did not show the slightest interest in his performance. This included not only a dazzling color display but also a loud stamping of the forelegs. When the female did not respond to a performance carried on only two feet in front of her head, the male flung himself on her back and secured a grip on the nape of her neck. This observation is in agreement with our laboratory studies on other lizards. It is the lizard which does not fight back that calls forth the mating response in the male. Female posturing has not been definitely proved in any lizard to have speeded up sexual union.

SCINCIDÆ

OBSERVATIONS ON EUMECES FASCIATUS AND E. LATICEPS

Many species of scincids exhibit a sexual dichromatism but this is usually not pronounced. Further, few are adorned with gaudy colors or are able to undergo rapid changes in tone. We might expect from what has been said above that they would make little attempt to bluff rivals. We have kept three species of *Eumeces* under observation for several months. As in most other lizards, the males alone fight. They attack one another with vigor, snapping at the snout of their opponents. When a male is attacked, he turns and with open mouth darts at the head of his annoyer. Females, according to our observations, always run away and hide. The struggles among the males are contests of strength and perseverence. There is never any flattening of the body and broadside approach as there is in the brilliant male iguanids. Correlated with this different method of fighting, male *Eumeces* when full-grown have a larger head and more powerful jaw muscles than lizards such as *Leiocephalus,* which lay so much emphasis on bluffing.

We observed eighteen copulations of *Eumeces fasciatus* and the closely allied *E. laticeps.* When we began our studies, the two species had not been clearly distinguished in the herpetological literature and we considered them one form. In later studies, where we distinguished the

two forms, no difference in behavior was noted and hence, for our purposes, they may be considered one form. Four of these copulations were with other males, nine with females and five with individuals whose sex was not determined. We observed eight courtships which did not end in copulation and six of these were with males. It, therefore, seems certain that male *Eumeces,* when maintained under the conditions employed in these studies, frequently cannot distinguish other males from females.

Only four to twelve lizards were kept together in a cage and each had a run of several times its own length. Although the conditions would not be described as crowded, they do not accurately represent the conditions under which the lizards live in nature. We have never seen in nature as many as half a dozen individuals of *Eumeces* living within a few square feet of space. Probably the males mark off territories as do other lizards but no field studies have established this fact. All that can be said at the present time is that, when several individuals of opposite sex are forced to live together within small confines, the males frequently copulate with other males. This seems to occur because the attacked lizard under these conditions fails to fight back with vigor.

Preliminaries of Courting

There is a marked difference between the approach of a male intent on copulating and one which is in the fighting mood. This suggests that males drive other males from their territories at one time and copulate with the non-resisting females that chance to enter these territories at other times. In the laboratory we have noticed on three occasions the male rubbed his cloaca on the ground as in *Ameiva* before seeking a mate. In one case a male scratched the ground nervously first with one hind leg and then with the other before starting out to court. *Eumeces* keeps under cover more than most lizards and this may be the reason that these preliminaries to mating were not observed more often. Another preliminary was noted once, and may have occurred in others: the male vibrated the end of his tail and looked about in search of a mate.

Subsequent Behavior

The next phase of courtship is very diagnostic. The male approaches any lizard of his own species near at hand and, instead of rushing at its head in the manner of a fighting male, he turns his head sharply and attempts to nip the other lizard on the side of the neck. If the approached lizard is a male, he opens his mouth and attempts to avoid these thrusts.

The courting male usually persists and together the pair circle about the cage, the bite of the male always directed at the other's neck.

The male *Eumeces* never takes a dorsal position nor rides on his mate's back as in the Teiidæ. He walks or runs beside her trying to secure the neck grip. When he finally secures a firm hold directly behind the ear opening, he begins to work his tail under hers to bring their cloacas together. This movement is accomplished by his placing both fore and hind feet of one side on the back of his mate (Fig. 1B). His weight is thrown on the two other legs, which remain on the ground. There is never any leg rubbing and it may be noted that these skinks have no femoral organs. There may, however, be considerable struggling during which the male presses down with his legs or moves his legs to prevent his mate from slipping away. As soon as the mate quiets and the cloacas have been brought in contact, the male protrudes the hemipenis on the side adjacent to the female. As he extends it, he pushes forward with his cloaca and pulls backward on the female's neck. The pair then usually lies quiet for a few seconds but in one case this extended over three minutes. Suddenly the male begins rhythmical forward and backward motions of his pelvis, causing the inserted hemipenis to move slightly in and out of the female's cloaca. These movements resemble those of *Cnemidophorus* but the motion is slower and the highly vascularized base of the hemipenis is usually visible.

If the female starts to move away, the male discontinues these rhythmical movements but retains his position on his partner's back. When the mate becomes quiet again, the rhythmical movements are resumed. These movements cause the side of the male's tail posterior to the cloaca to rub the ventral surface of the base of the female's tail. On two occasions the male retracted his hemipenis and began the rhythmical motions again while maintaining his grip on his partner's neck. The female remained quiet and it is possible that the rhythmical pressing of the male's tail base against that of the female served to quiet her. This false copulation once occurred after a six-minute copulation with a female, during which rhythmic movements lasted two minutes. Another such performance occurred after a seven-minute copulation with a male, during which rhythmic movements were observed for one minute. Rhythmical movements, therefore, occur whether or not the hemipenis of the male is withdrawn from the cloaca of the partner.

In the eighteen copulations of *Eumeces fasciatus* witnessed by us the coitus lasted from four to eight minutes while courtship required from five to seven minutes.

Burt (1928) has described the copulation in *Eumeces obsoletus*. It agrees essentially with that of *E. fasciatus* except that no rhythmical movements of the pelvis occur. We have witnessed one courtship and another mating in this species. The courtship was evidently between males since they circled the cage endeavoring to secure the neck grip on one another. The mating was with a female. Coitus lasted three minutes, while Burt (op. cit.) gives about four minutes for his record.

In conclusion we give the records of one mating in *Eumeces fasciatus* as observed by us in the laboratory. This may be considered typical of the genus although it differs from the above description in a few details.

A Typical Mating of Eumeces

March 30, 1931. Room temperature 82° F.

In the morning a small male of *E. fasciatus* attempted to mate with another that appeared to be a male. At noon another small male only 61 mm. in head and body length seized a female 64 mm. in head and body length on the back just above the right arm. This was apparently a case where the male failed to secure his usual grip on the side of the neck. The male's head was only slightly red, not strikingly different from that of the female. The female struggled but the male shook the female, carrying her body from side to side at the rate of approximately three twists a second. There was at least a dozen of these movements. While thus engaged the male did not move his pelvis from side to side nor vibrate the end of his tail. When the female gave up struggling, the male pushed his tail under that of his partner from the right side, at the same time keeping his left leg firmly across her back. There were no rubbing movements of either leg. He supported his weight on his two right legs, while his two left legs pressed her down. He then directed his cloaca forward until it nearly met hers. At this moment his left hemipenis was partly everted and he thrust it forward as it entered her cloaca. While the distal half of the hemipenis was enclosed by the cloacal lips, the base was clearly visible to the observer. Both lizards ceased to struggle and there was no movement for three or four minutes other than the rapid respiratory vibrations of the two lizards. Soon the male began rhythmical forward and backward movements of his pelvis, while the anterior part of his body remained still. His left leg firmly gripped the partner's back and moved slightly backward at each forward movement of his cloaca and in the reverse direction at each backward movement of the same. His tail base was held against the base of the female's tail and the cloacal movements caused it to rub her in that region. The cloacal movements continued for about two minutes.

Then the female began to move away and the male ceased his movements but retained his hemipenis within the female's cloaca and his grip on her neck. A moment later the female stopped moving but continued to breathe heavily. Slowly the male withdrew his hemipenis, retracting it within his tail base. The same rhythmical movements of the cloacal region began again and the base of the male's tail rubbed that of the female as before. She did not move as these continued for two minutes. The male then released his neck grip and the female moved slowly away. The male remained behind and did not move while the female was picked up, sexed and measured. Microscopical examination revealed sperm in a cloacal smear taken from the female.

Although the mating of no other scincid is known in this detail, it is probable that all species of the family conform to this behavior pattern. Fischer (1882) has described the male *Gongylus ocellatus* as securing a grip on the ear region of the female. *Tiliqua scincoides* grasps the female by the back of the neck (Senftleben, 1914) and apparently throws his tail under hers. The enlarged scale found by Gandolfi (1907) on the soles of the hind feet of *Lygosoma smaragdinum* may serve to hold the female down as no scincid has been reported to practise rubbing movements.

ANGUIDÆ

We have had the opportunity of keeping very few anguids in our observation cages and only in one case did we observe any behavior which might be interpreted as courtship. On several occasions we observed a male *Celestus costatus* seize a female's snout in his jaws. The pair would then walk side by side around the cage, the male retaining his grip on the female's head and occasionally scratching her back with the claws nearest to her. At other times he would snap his body in an arch over hers while maintaining his grip on her snout. This tendency to encircle the female's body is suggestive of the courtship of the Teiidæ but the grip was never inguinal as in that family.

THE MATING OF ANGUIS IS LIZARD-LIKE, NOT SNAKE-LIKE

One male retained his grip on a female from three o'clock one day until noon the next. This prolonged hold on the mate may be an anguid characteristic. Meyer (1874) reported that the male *Anguis fragilis* seizes the female violently by the back of the head with his teeth and remains for several hours with his cloaca adpressed to that of the female. Klingelhöffer (1931), however, gives the time as approximately half an hour. Unfortunately we never witnessed a coitus in our courting *Celestus* and it may,

in fact, never have occurred. Hence we cannot be sure that the behavior described above is a part of the normal courtship of *Celestus*.

It may be emphasized that *Anguis fragilis* in spite of its snake-like form does not mate in the manner of snakes. During copulation it retains the neck grip which is the most widespread posture among mating lizards. Although a few snakes have been reported to seize the female in their mouth, rubbing and entwining movements form the greater part of their courtship. Such body movements are unknown in lizards. According to Klingelhöffer the body of *Anguis fragilis* is bent in a semicircle during mating. Although *Anguis* has undergone extreme specialization of body form, it retains the mating habits of other primitive families of lizards.

OTHER FAMILIES OF LIZARDS

In the scattered literature dealing with the behavior of lizards in captivity there is frequent brief reference to mating. Werner (1893) makes it clear that *Varanus griseus* seizes the female by the neck. This appears to be the copulation posture assumed by the majority of lizards. As we have shown above, where divergencies from this pattern occur, they are usually common to natural groups of species.

THE MATING BEHAVIOR OF CHAMELEONS

There is at least one other copulation posture found in a natural group of lizards which we have not mentioned above. The true chameleons of the Old World have specialized for arboreal life and their feet and tail are highly prehensile organs. Klein (1931) has recently described the copulation in *Chamaeleon chamaeleon*. The male seized the neck of the female in his teeth and released the grip as soon as he had secured a firm grip with all four feet on her body. *Chamaeleon calcaratus* apparently seizes the female directly with all four legs (Trench, 1912). Long ago Fischer (1882) gave an extensive account of the mating in *Chamaeleon chamaeleon*. In this case the male, which Fischer described in great detail, did not use its teeth but followed the female about until it caught her with one front foot in the neck region. Whereupon he placed his other fore foot on the back of the female while his hind feet embraced her knee and tail. The female struggled and attempted to free herself by dragging the male about the cage. During copulation, which lasted from a few seconds to fourteen minutes, there were "erotische Bewegungen." It is possible that it will be found that some other lizards, such as *Phrynosoma,* have given up the use of the jaws in holding the female, but the chameleon's method of using its limbs is very different from that of other

lizards and would only be possible in a species with highly prehensile appendages.

The true chameleons are notable for their remarkable color displays. It is, therefore, of interest to inquire further into the known facts of their courtship, for, if color is of value in stimulating the female to mate or to find males, as previous authors have suggested in the case of other gaudy lizards, we should see some evidence of it in this group.   We may follow first Fischer's (op. cit.) account, which is not only one of the oldest but one of the most detailed.   As the breeding season approaches, the chameleons, which have been living peacefully together, become very pugnacious.   They inflate their bodies, lift themselves on stiff legs and rivals advance broadside toward each other.   This is not mere bluff, for they butt severely with the sharp edges of their casques.   It may be noted that the only lizards which have been reported to butt with their heads during fights have heads ideally built for this function. *Iguana* assumes a butting attitude and has a rounded, heavily scaled forehead. Chameleons which give vicious head thrusts either have sharp edged casques or various types of horns.   In *C. owenii* the males have three horns on the upper surface of the head and these have bony cores, which are ankylosed to the skull.

C. chamaeleon without the horns and with only the bright color and casque for fighting equipment is, however, able to hiss loudly on both inspiration and expiration.   Fischer makes it clear that it is the male which seeks the opposite sex.   He describes males intent on mating following every animal that comes in their way without regard to kind or size. One male followed a *Clemys*, 5 cms. long, into the water, seized it with his forefeet and pulled it out of the water.   He also attempted to mate with agamids and skinks.   In any lizard which has such poor powers of discrimination the males would frequently mate with other males were it not that the male, when approached during the breeding season, responds with the fight reaction.

Fischer (op. cit.) does not describe the female *Chamaeleon* as showing a sexual interest in the male.   Klein (op. cit.) gives a detailed account of the beginning of courtship in *C. chamaeleon*.   The male "was sitting quietly on a branch when suddenly, contrary to its usual demeanor, it turned toward the large specimen with a lizard-like quickness, lashing its curved tail in the air, threw itself rapaciously upon the large animal and with its teeth seized the victim by the neck. . . ." (translation). Copulation followed as soon as the male had secured a firm grip with its four limbs.   From this description it is clear that the male makes no

attempt to arouse the interest of the female before mating. As in other lizards, the color display is reserved for the fights. Some female chameleons (Fischer, op. cit.), like some *Leiocephalus,* are able to fight but apparently a fight reaction is not usually aroused in them by the advances of a courting male.

Loveridge (1923) has described a female *Chamaeleon dilepis* as gently biting the male but, as this lizard had its hind limbs and part of the tail partially paralysed, the gesturing may have been as Loveridge writes "somewhat abnormal."

Unfortunately no data is available as to the territories occupied by chameleons in the field. Since the males are pugnacious they probably do not tolerate other males in their immediate vicinity.

THE FUNCTIONS OF BRIGHT COLORS IN CHAMELEONS

The bright colors of chameleons have a wide variety of functions besides those of display. Color change is rapid and many of the tones are highly protective to a lizard living on an exposed tree. Color change is induced by a variety of external and internal conditions. It is a significant fact that fighting chameleons turn their colorful sides toward opponents, while courting males do not give the females equal opportunities for gazing upon the bright tones which their excitement may have induced. We may conclude that in the chameleons a color display does not represent a method of sex attraction but it facilitates sex recognition by aiding males in repelling other males.

THE FIGHTING BEHAVIOR OF GECKOS

Not all lizards show a sexual dichromatism. Those which have succeeded without this bluff mechanism in the male are often persistent fighters. This is especially true of the nocturnal geckonids. Fischer (1887) has given a vivid description of the fighting between the males of several genera. Geckos apparently have well defined territories even in the terrarium. Fischer finds that a male *Hemidactylus* or *Gymnodactylus* placed in a cage already occupied by these geckos is relentlessly attacked by the occupants of the cage.

Geckos, like many other nocturnal creatures, are endowed with a voice. They give vent to various sounds while fighting. Possibly these cries, like the hissing of chameleons, can be considered a terrorizing device. Loveridge (1923) heard the cry of a gecko and, immediately following the sound, he saw a pair of *Hemidactylus mabouia* mate. However, Parshad (1916) witnessed the mating of *Hemidactylus flaviviridis* under

especially favorable circumstances but heard no vocal display. It is an attractive hypothesis that nocturnal geckos, like nocturnal frogs, call the females to them from afar. Unfortunately, while the movements of a female frog toward a calling male have been watched, no such observations have been made on geckos. In fact, the whole mating process in geckos is poorly known.

THE COURTSHIP AND MATING OF GECKOS

Geckos are primitive lizards and it is not surprising that all species, so far as known, seize the female by the neck in order to copulate. In *Hemidactylus flaviviridis* according to Parshad (op. cit.) there is more of a courtship than has been described in any other lizard. In the one mating which Parshad observed in detail the male moved around the female in circles, frequently touching her with his head or tongue. When the female turned her head toward the male, he secured a firm hold. The female apparently voluntarily raised her tail, permitting the male to bring the cloacal apertures together. Mertens (1929) also described in *Ptychozoon kuhli* a prolonged performance which had the appearance of courtship although it did not end in copulation. The male moved his tail in a peculiar manner and gave short cries. The female also moved her tail in a lively manner apparently in response to his actions.

It is possible that geckos, being chiefly nocturnal creatures, have built up a type of courtship different from all other lizards. However, the copulation posture is the same as in other primitive lizards. The mating of the brilliant diurnal geckonids is still unknown and except for Parshad's single observation the early stages in the courtship of no gecko has been described.

SUBCAUDAL SACS OF CERTAIN GECKOS

Observations on the courtship of geckos may shed light on a peculiar secondary sexual character whose function at the present time is unknown. So long ago as 1876, Wiedersheim observed a pair of gland-like orifices on the ventral surface of the tail base of *Phyllodactylus europaeus*, which he briefly compares to femoral organs. Homologous structures are found in many genera of gekkonids and have been well figured by various investigators such as Taylor (1922). Very few students mention these structures by name, and none, so far as we are aware, have discussed their probable function. Deraniyagala (1932) states that in *Hemidactylus brooki* the "two subcaudal glands are conspicuous." We have studied these structures in this species and in living *Tarentola,*

Thecadactylus and *Coleonyx*.   They are absent in *Sphaerodactylus, Aris-
telliger, Aristelligella* and some other genera.

We have studied sections of the subcaudal sacs in *Phyllodactylus euro-
paeus* and *Coleonyx variegatus* and have seen no evidence of glandular
activity in the squamous epithelium lining each sac.   The sacs are much
larger in the male than in the female of all geckonids we have examined.
In *Thecadactylus rapicaudus, Tarentola mauritanica* and probably in other
species the lining of the sac is shed with the remainder of the skin at the
time of molting.

A clue as to the probable function of the sacs was obtained in a series
of healthy *Tarentola mauritanica*.   Rubbing the lateral margins of the
caudal lip of the cloaca of either sex with a dull instrument will cause
both sides of this lip to be drawn caudally.   In the male it also causes the
posterior part of the skin inside the sac to be drawn caudally and at
the same time the orifice of the sac is opened widely, the cavity extending
caudally and slightly dorsally.   The fact that the loose skin, present
inside the sac in males, can be pulled out of the sac without causing any
reaction on the part of the lizard leads us to believe that the sac has no
sensory function.   Immediately upon touching the caudal cloacal lip this
skin is jerked inward and caudally, and the orifice gapes widely open.
Once open, the sac does not immediately close, although the cloacal lips
may relax.   The orifice of the sac will close suddenly if the animal is
touched or pinched in other parts of the body, or even on the tail in the
vicinity of the sac.

In this and some other geckos there is a bone transverse to the tail lying
on the anterior margin of each sac.   One of us (Noble, 1921) has given
the structure the non-committal name of "cloacal bone" since it is present
in some forms which lack the sacs.   The bone in the male *Tarentola*
apparently aids in making the orifice gape widely.   In the female rubbing
the lower lip of the cloaca brings only the response of drawing back the
sides of that lip and so closing the small orifices present.   Hence, it would
appear that these are rudimentary structures and probably without func-
tion in the female.

In the mating of *Eumeces fasciatus,* a lizard whose copulation pos-
ture is the same as that of the gekkonids, it was pointed out that the male
may continue to press rhythmically the ventral surface of his tail base
against that of the female even after his hemipenis has been withdrawn.
During this false copulation the female remained quiet.   In *Tarentola*
a similar movement would cause the subcaudal sacs to gape open, pro-
ducing a slight vacuum.   Such action would probably have the same

stimulating effect as the rhythmical movements in *Eumeces.* It is, therefore, highly probable that the subcaudal sacs are stimulating organs which tend to quiet the female during the act of copulation.

SEXUAL SELECTION IN LIZARDS

It has been shown above that lizards of several families, when kept in good health in large laboratory cages, court and frequently copulate with other males. Since the cloaca of a male lizard permits the insertion of the hemipenis of another male, there is no structural hindrance to this performance. The only mechanism which is present to prevent males copulating with other males as frequently as with females is that males when meeting each other during the breeding season tend to fight. The result is that males tend to occupy discrete territories, which are difficult to recognize in the laboratory but which have been described in the field. In the laboratory, males of species such as *Ameiva,* which seldom fight or do not fight at all, copulate with other males. But even species such as *Anolis,* which fight nearly every day, average a high percentage of homosexual unions. This is apparently due to the fact that in the confines of a laboratory cage the seized male does not have time to advertise his sex by a defense reaction against the aggressive male or by the fact that in some cases he is too weakened to do so.

THE FUNCTION OF BRIGHT COLORS IN THE MALES

The bright colors of many male lizards have been shown above to function not in stimulating females to breed but in frightening away rival males. In those species which have gaudy males there is never an extreme display before the female. Such displays are reserved for the fights during which the male frequently walks sideways toward his opponent, flattening his body in a vertical plane and often erecting fleshy crests or dewlaps to their maximum extent. Bobbing or "hobby horse" movements, such as those of *Leiocephalus,* often make these displays seem ludicrous. Nevertheless the bluffing is effective, for some of the most ornate males rarely have to use their teeth in driving away a rival. Conversely, the males that are not bedecked with bright colors do not compress their bodies or keep themselves broadside to their opponent when making an attack. They use their teeth to good advantage on such occasions.

Sexual displays of color or movement frequently call forth similar displays in nearby males but females in all the species studied by us in the laboratory remain unmoved by these performances. Our work was

carried forward with five species of *Anolis,* two of *Leiocephalus,* two of *Ameiva,* two of *Euineces,* one of *Cnemidophorus* and one of *Sceloporus.* We could secure no evidence of their being attracted by either the extreme fight displays or by the less complete demonstrations of color, movement or size which sometimes precede courtship.

The evidence for these statements is to be found in the foregoing sections. Since females are not attracted while males are definitely repulsed by color displays, it follows that female choice has played no part in the genesis of male adornment. The extreme specialization of color in male lizards would seem to owe its origin to the conservation through natural selection of those males that could most successfully bluff their rivals. Natural selection would tend in time to give strength or size to the males in those groups which attack with teeth, and it would enhance the color or other bluffing devices in the males of those groups which rely to a large extent on being able to frighten their rivals.

DEFENSE OF TERRITORY DURING THE BREEDING SEASON

Field studies have shown that many lizards live in circumscribed territories which the males defend during the breeding season. Newman and Patterson (1909) found that in one species of *Sceloporus* the males wander during the breeding season and take up new territories where they remain during most of the year. A female may remain with the male in this territory but, to judge from the behavior of lizards in general, there is no reason to assume there is any psychical bond which holds the pair together. It is more likely from the data presented above that, since the female does not fight, she does not call forth the fighting response when the male chances during the breeding season into her territory, or she into his as the case may be. Consequently, they are able to live together in peace, which breeding males of most species of lizards are unable to do. Once the season has passed, the pair settles down to live in the nearest suitable territory. In at least one species of lizard the young also remain in restricted territories until sexual maturity, and here the tendency of lizards to remain on familiar grounds must be strongly developed at an early age.

THE COURTING AND THE FIGHTING REACTIONS

The courting behavior of lizards, as pointed out above, is a very stereotyped performance, often diagnostic of natural groups of genera. It is not to be confused with the fighting reaction, which is less stereotyped and often more spectacular. The courting and fighting reactions usually do

not follow each other closely although we have pointed out some excep-
tions.   The winner of a fight never copulates with the male he has con-
quered although he may later, when dominated by the mating instincts,
copulate with the same male if the latter does not defend himself ade-
quately.   The fighting response leads, therefore, to an acquisition of
territory, not of a mate, while the courting reactions lead to the securing
of a mate, which would be of the same sex as the master of the terri-
tory were it not for the fact that males usually respond to the attack
of another lizard with the fight response.

<div align="center">THE FAILURE OF AMEIVA TO EXHIBIT THE FIGHT REACTION</div>

Of the several genera of lizards studied by us in the laboratory only
Ameiva fails to exhibit the fight reaction.   Whether males of this genus
frequently mate with other males in nature is not known, but it is pos-
sible that with a larger area of escape they would be better able to avoid
the advances of other males even though they do not fight.

From the data at hand we may assume that sex recognition is accom-
plished in *Ameiva* by trial mounting.   Some mammals such as the guinea-
pig (Loutitt, 1927) may determine whether the female is in oestrus by
trial mounting but sex discrimination is made usually before mounting.
Since *Ameiva* will copulate with immature females and with males, there
is obviously no oestrus in the sense of a response on the part of a female
before copulation can occur.   Sex recognition in most lizards is accom-
plished merely by response of an approached individual to the aggression
or partial display of a male.   In *Ameiva,* if sex discrimination is made at
all, it probably rests on the ability of the male to better defend himself
against copulation.

<div align="center">THE MATING BEHAVIOR OF LIZARDS COMPARED WITH THAT OF BIRDS</div>

The mating behavior of lizards has a considerable resemblance to that
of birds, especially to those with definite territories.   In both, the males
migrate during the breeding season into new territory, which they defend
against rival males.   The females that enter this territory are not mo-
lested.   Only later do the courting reactions develop.   How much later in
lizards is not known in detail.   A fundamental difference between the
mating of lizards and that of birds is that the male lizards can mate with
females at any time their own mating instincts develop.   There is no
waiting for an oestrus in the female such as Howard (1929) described
for birds.   Another important difference, already noted above, is the
ability of male lizards to copulate with other males.   This they do fre-

quently in the laboratory but it has not yet been reported in nature and probably for the good reason that matings are seldom seen with any detail under natural conditions. The most significant difference is that lizards reserve their extreme displays for fights and not for courtships. Hence, in lizards natural selection has improved sexual differences in color to aid in bluffing rival males and not to help in stimulating the females to mate.

FORM AND FUNCTION OF THE HEMIPENIS

It has been shown above that natural groups of lizards are in many instances characterized by a single type of copulation posture. The form of the hemipenis has also been claimed to define natural groups (Cope, 1900). It would seem to follow that a particular type of hemipenis was correlated with a particular mode of mating. We have shown, for example, that *Ameiva* and *Cnemidophorus* have the same method of copulation, which is readily distinguished from the modes practised by lizards of other families. Burt (1931), the most recent reviewer of the latter genus, comments:

> There is apparently no difference in the penial structure of *Cnemidophorus* and *Ameiva*.

SPECIFIC AND GENERIC VARIATIONS IN THE FORM OF THE HEMIPENIS

We have studied the hemipenes of a series of lizards injected with salt solution and fixed in 10 per cent formalin. As shown in Figs. 10 A and E, we find a considerable specific variation of the form of the hemipenis within the genus *Ameiva* and a marked difference between the hemipenis of *Ameiva chrysolaema* and *Cnemidophorus sexlineatus*. The hemipenis of *A. chrysolaema* has a superficial resemblance to that of *Lacerta ocellata* but, instead of there being a triangular welt of dense tissue at the distal end of the *sulcus spermaticus*, there is a bilobed welt on each side in the same position. There is a series of transverse folds on the hemipenis of both species but these are larger in *Ameiva* and they extend farther proximally toward the base of the organ.

In *Ameiva exsul* the larger and more proximal of the lobes of the terminal welt is emarginate, with the result that there appear to be three welts at the end of the sulcus on each side. On the opposite side of the hemipenis there is a longitudinal depression free of transverse ridges. In *Ameiva maynardii* this area is better marked off as a distinct furrow devoid of transverse ridges. The terminal welt is more distinctly trilobed. In the series *Ameiva chrysolaema-exsul-maynardii* there is a pro-
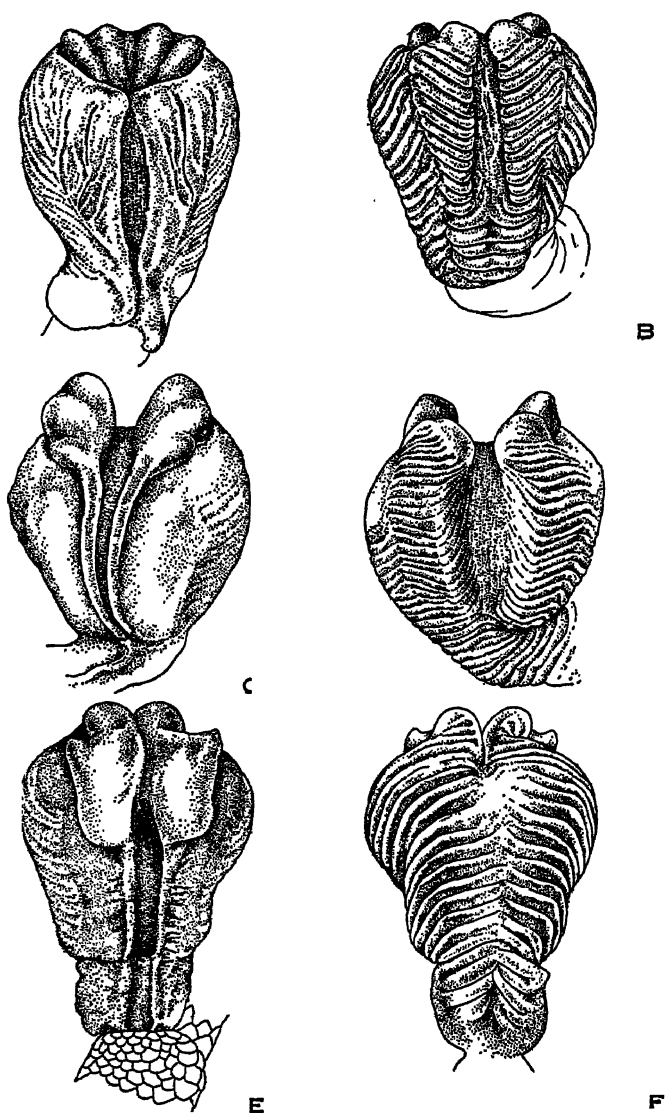
FIGURE 10.—The hemipenes of teiid lizards.

A.—*Cnemidophorus sexlineatus,* mesial aspect, *sulcus spermaticus* in the midline.

B.—*Cnemidophorus sexlineatus,* lateral aspect.

C.—*Ameiva maynardii,* mesial aspect.

D.—*Ameiva maynardii,* lateral aspect.

E.—*Ameiva chrysolaema,* mesial aspect.

F.—*Ameiva chrysolaema,* lateral aspect.

gressive tendency toward the formation of a three-lobed welt at the end of the *sulcus spermaticus* and a groove devoid of cross ridges on the opposite side of the hemipenis.

In *Cnemidophorus sexlineatus* the transverse ridges are arranged in a series of everted v's (Fig. 10B) and the groove is better defined than in *Ameiva*. The head of the hemipenis appears to be deeply folded. This is not due to the fact that the hemipenis is not fully distended. When the head is dissected, the two lateral prominences are found to be formed by a pair of tubercles separated by a groove from the medial pair. The two pair do not form part of a fibrous welt as in *Ameiva*. There is, thus, a fundamental difference between the head of the hemipenis of *Cnemidophorus sexlineatus* and that of any of the species of *Ameiva* which we have examined in injected material.

It seems to us that this fact is of considerable significance and for two reasons: in the first place, *Ameiva* and *Cnemidophorus* are known to be closely related and yet they may differ considerably in the form of their hemipenis; in the second place, *Ameiva* and *Cnemidophorus* presumably sprang from a common ancestor and, while various structures such as the tongue and hemipenis have undergone morphological change, the mating pattern has nevertheless remained practically the same. Inherited habit may, therefore, be less liable to evolutionary change than many structural characters.

FORM IN RELATION TO FUNCTION

In the Iguanidæ there appears to be some correlation between the form of the hemipenis and its function. In *Anolis,* which usually retains its position of coitus longer than do the other species of this group, the head of the hemipenis is broader in relation to the base than in any of the other iguanids studied. Further, there are numerous transverse ridges, which would presumably tend to retain the hemipenis within the cloaca during copulation. Cope (1900, p. 196) states in regard to the hemipenis:

The higher *Sauria* have the apical parts modified as in the *Ophidia* by the presence of calyculi. Such are characteristic of the *Rhiptoglossa* and *Pachyglossa*. The *Nyctisaura* possess the same feature. The *Diploglossa, Helodermatoidea*, and *Thecaglossa* have the organ flounced, the flounces often pocketed or repand on the margin.

As shown in Fig. 11F, there are many ridges on the hemipenis of *Anolis* although these tend to break up into a transverse pitting on the head.
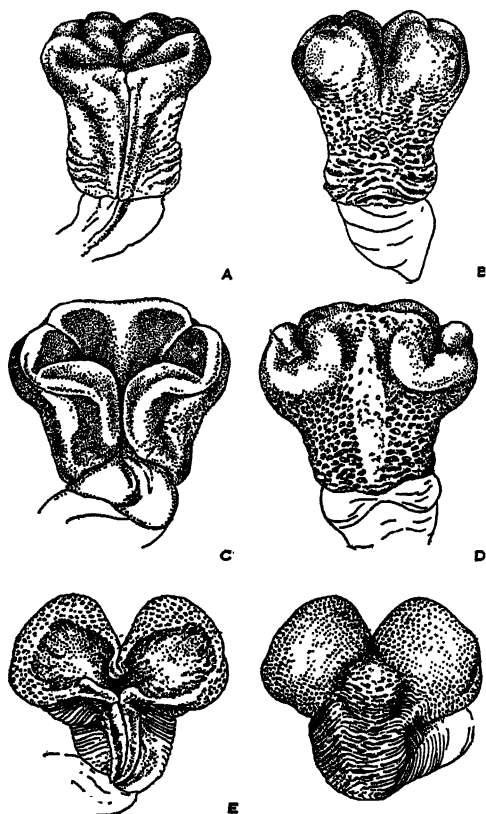
FIGURE 11.—Hemipenes of iguanid lizards.

A.—*Leiocephalus inaguae,* mesial aspect, *sulcus spermaticus* in midline.

B.—*Leiocephalus inaguae,* lateral aspect.

C.—*Sceloporus undulatus,* mesial aspect.

D.—*Sceloporus undulatus,* lateral aspect.

E.—*Anolis carolinensis,* mesial aspect.

F.—*Anolis carolinensis,* lateral aspect.

The two genera of iguanids studied by us which practice the shortest copulation have smaller heads to their hemipenes than do the other genera. It would seem that the plunger-like hemipenis of these two species was better fitted to be inserted and withdrawn rapidly than is the hemipenis of *Anolis.* In *Cnemidophorus,* however, the head of the hemipenis is also small and yet this lizard normally practices a long coitus. Hence, the correlation between the form of the hemipenis and the length of coitus applies only to the family Iguanidæ.

THE HEMIPENIS OF IGUANIDÆ

The hemipenis in the various iguanids studied exhibits a considerable variety of form in spite of the constancy in copulation posture exhibited by these species. In *Anolis carolinensis* on the side opposite the *sulcus spermaticus* there is a prominent swelling. In *Sceloporus* this swelling is replaced by a longitudinal strip of dense tissue. In *Leiocephalus* the same part of the hemipenis is covered merely with the honey-comb structure found on most of the hemipenal stalk (Figs. 11B and 11D). Other differences appear in the apices of the hemipenes of the three species fig-

A
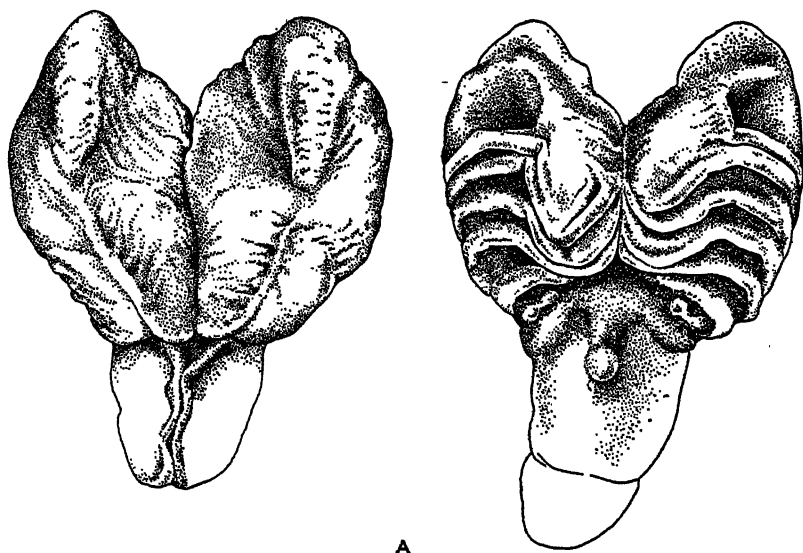
FIGURE 12.—Hemipenis of *Eumeces fasciatus.*

A.—Mesial aspect.

B.—Lateral aspect.

ured. Whether or not these differences have a systematic value will have to await the detailed study of the hemipenes in a large number of iguanid genera.

THE HEMIPENIS OF SCINCIDÆ

Cope (op. cit., p. 617) states in regard to the Scincidæ:

I have examined the hemipenis in *Trachysaurus, Lepidothyris (fernandi), Euprepes (carinatus), Eumeces* and *Mabuia.* They are smooth and with more or less numerous longitudinal folds, excepting in *Trachysaurus.*

We have examined the injected hemipenes of two species of *Eumeces,* namely *E. fasciatus* and *E. obsoletus.* They are essentially alike and differ from the hemipenes of all other lizards employed in this study in being formed of less fibrous tissue on the side opposite to the *sulcus spermaticus.* The head is proportionately large and a broad, heart-shaped pad of dense tissue covers it on the side of the *sulcus spermaticus* (Fig. 12A). Contrary to Cope's statement there are no longitudinal folds in the fully distended hemipenis but a series of transverse flounces are present on the side opposite the heart-shaped pad. These transverse ridges are better developed in *fasciatus* than in *obsoletus.* At the distal end of the stalk of the hemipenis is a prominent tubercle of soft tissue (Fig. 12B).

In view of the fact that the hemipenal structure is known in so very few scincids it would be unwise to generalize, as Cope has done, regarding the systematic significance of these differences. It may be noted, however, that the hemipenes of the Scincidæ and Iguanidæ are less complex than those of the Teiidæ and Lacertidæ so far as known. Moreover, the mating behavior of the first two groups is more generalized than is that of the two latter families.

CONCLUSIONS

The courtship and mating of lizards is a very stereotyped performance, which has changed slowly in phylogeny. A single type of performance is usually found throughout a natural group of species or genera.

The mating behavior develops spontaneously in males and is directed toward other individuals regardless of sex. Male lizards of most species fight during the breeding season, and this response of the male, when approached by another lizard, forms the basis of sex discrimination.

Under laboratory conditions where an approached male does not have the opportunity of responding with a fight reaction, males frequently copulate with other males. Under these circumstances the pattern of courtship and of mating is the same as when a male mates with a female.

The bright colors which adorn many male lizards do not serve as attracting devices as has been assumed hitherto. Neither females nor males are attracted by the displays. Bright colors have the important function of aiding in sham fights when the males attempt to avoid combat with rivals by making themselves appear as large and conspicuous as possible. The greatest displays of color are directed toward rival males, and not toward females.

   Since male lizards of most species fight during the breeding season, lizards tend to live in definite territories during that season at least. Bright colors have aided in the maintaining of territory against rival males.

   Lizards which practice the same type of mating performance may have strikingly different hemipenes.   The species, however, that have the more complex performances have the more modified hemipenes.

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MIMOSACEÆ AND CÆSALPINIACEÆ OF COLOMBIA

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PREFACE

By E. P. KILLIP

With the completion of their studies of cacti and the publication of the monograph "The Cactaceæ," Doctors N. L. Britton and J. N. Rose began the preparation of the Mimosaceæ and Cæsalpiniaceæ portions of the North American Flora. This work naturally involved a survey of the species of northern South America, in the course of which descriptions of several new species were drawn up on the basis of the collections of the many American botanists then exploring British Guiana, Venezuela, Colombia and Ecuador. An enumeration of the northern South American species of these two families was contemplated.

Dr. Rose died in 1928 and Dr. Britton continued the work. In 1931 he invited me to join him in preparing an account of the Colombian species. The present paper was completed shortly before Dr. Britton's death, in June, 1934. In making a final revision of the manuscript I have substituted, in five instances, conserved generic names for those used by Dr. Britton, and have inserted Latin diagnoses—both changes made in order to conform to the recently adopted International Rules of Botanical Nomenclature. I have been tempted to use other names for the species that Britton, or Britton and Rose, had named in my honor as the collector but, in view of the fact that duplicate material of many of these had been widely distributed among herbaria, I have felt that only confusion would result if this course were followed.

INTRODUCTION

Its geographical position, wide range in altitude and striking topographical features combine to give the Republic of Colombia a highly diversified flora. Situated in the northwestern corner of the continent, it alone of South American countries fronts upon both the Caribbean Sea and the Pacific Ocean. Its mountains reach heights of more than 18,000 feet and, between sea level and the snowline, there are the dense forests of the tropical and subtropical zones, the temperate vegetation and the alpine flora of the higher mountain plateaus, called in the Andes *páramos*.

Just north of the Ecuadorean boundary the Andes divide into three well-marked, nearly parallel cordilleras, of which the Eastern in turn forks near Bucaramanga, one branch extending due eastward into Venezuela, the other running a short distance northward in Colombia; the Central and the Western cordilleras continue northward until they slope down to the Caribbean coastal region. These main cordilleras are separated by two great river valleys, the Magdalena, between the Eastern and the Central ranges, and the Cauca, between the Central and the Western. In the extreme northeastern corner of the country lie the isolated Santa Marta mountains. The southeastern part of the republic, constituting nearly one-half the total area of the country, lies in the basins of the Amazon and the Orinoco rivers.

BOTANICAL EXPLORATION IN COLOMBIA

Botanical exploration in Colombia has been extensive but, though our knowledge of certain areas is fairly adequate, many portions are still imperfectly known. ·The greater part of the collecting has been done in the Bogotá and Popayán regions, in the Magdalena and Cauca valleys, and in the northern coastal area. The vast stretches east of the Eastern Cordillera are almost wholly unknown botanically.

The extensive botanical work carried on in Colombia during the 18th and 19th centuries may be shown by the following list of collectors arranged in the sequence of their investigations:—

Jacquin, Nikolaus Joseph von, 1727-1817. Cartagena.
Mutis, José Celestino, 1732-1808. Mainly in the vicinity of Bogotá and Mariquita.
Humboldt, Friedrich Heinrich Alexander von, 1769-1859, and Bonpland, Aime Jacques Alexandre, 1773-1858. Cartagena, Magdalena Valley, Bogotá, Quindío Trail, Cauca Valley to the Ecuador border.

Bertero, Carlo Giuseppe, 1789-1831. Santa Marta.

Goudot, Justin. Mainly Bogotá, upper Magdalena Valley, and Quindío Trail.

Triana, José Jeronimo, 1834-1890. Traveled extensively in Colombia, his more important collections coming from the Bogotá region. Quindío Trail, Chocó, Cauca Valley, and the southwestern parts.

Karsten, Gustav Karl Wilhelm Hermann, 1817-1908. Mainly in eastern Colombia.

Hartweg, Carl Theodor, 1812-1871. Southwestern Colombia and Cundinamarca.

Holton, Isaac Farwell, 1812-1874. Mainly about Bogotá and in the Cauca Valley.

Funck, Nicolas, 1816-1896, and Schlim, Louis Joseph. Eastern Colombia, especially in the departments of Santander and Norte de Santander.

Linden, Jean Jules, 1817-1898. Departments of Santander, Norte de Santander, Cundinamarca and Tolima, and in the Santa Marta mountains.

Purdie, William, 1817-1857. Santa Marta mountains.

Kalbreyer, Wilhelm (Guillermo), 1847-1912. Eastern Cordillera and Antioquia.

André, Edouard François, 1840-1911. Magdalena Valley, Bogotá. Quindío Trail, Cauca Valley to the Ecuador border.

Stuebel, Moritz Alphons, 1835-1904. Southwestern Colombia.

Lehmann, Friedrich Carl, 1850-1903. Mainly in the Central and Western cordilleras and the Cauca Valley.

Among European collectors who in the present century have visited Colombia the following should be mentioned: T. A. Sprague and G. Voronoff, whose collections afford almost our sole knowledge of the flora of Amazonian Colombia; M. T. Dawe, who collected in Cundinamarca, Boyacá, Goajira and the Magdalena Valley; J. Cuatrecasas, in the Quindío and Cundinamarca; Frau E. Dryander, in the Cauca Valley; C. Troll, in Cundinamarca; A. Schultze, in Cundinamarca and the Santa Marta mountains; E. Langlassé, in western Colombia; Mrs. J. A. Tracey, in Cundinamarca; and Cyril Allen, in the Magdalena Valley.

Botanists resident in Colombia, whose collections are well represented in herbaria of the United States, are Brothers Apollinaire Marie and Ariste Joseph (largely from Cundinamarca and the Meta), E. Pérez Arbelaez (Cundinamarca, Caquetá and the Meta), B. Guevara Amor-

tegui (Cundinamarca and Boyacá), Brother Elias and A. Dugand (Department of Atlántico), Brother Heriberto (Cartagena and vicinity), Brother Daniel (Medellín). Dr. A. Ducke, well-known student of the Amazonian flora, has made collections in the Caquetá Valley, in the southeastern part of Colombia. The 375 specimens collected in the Putumayo Valley, in southeastern Colombia, by G. Klug, of Iquitos, Peru, and widely distributed to American and European herbaria, are of great importance.

As a result of a program for the botanical exploration of northern South America, made by several institutions of the United States, three expeditions have been sent to Colombia, their collecting numbers totaling more than 19,000. The Rusby-Pennell expedition of 1917 visited the northern coastal region, the Magdalena Valley, and the departments of Cundinamarca, Huila, Tolima and Antioquia, and the Meta. The Pennell-Killip-Hazen expedition of 1922 explored the western litoral, the Central and Western cordilleras, and the Cauca Valley. The Killip-Smith expedition of 1926-1927 worked in the Cartagena-Turbaco region and the departments of Santander and Norte de Santander.

Other important collections made by North American botanists or by botanists collecting for institutions of this country are those of H. H. Smith, in the Santa Marta region; H. Pittier, in western Colombia; W. A. Archer, in Antioquia and the Chocó; R. A. Toro and C. E. Chardon, in Antioquia; H. M. Curran, in the lower Magdalena Valley and about Cartagena; A. E. Lawrance, in Boyacá; and W. Seifriz, the only American botanist to explore the higher mountains of the Santa Marta group.

BASIS AND SCOPE OF THE PRESENT STUDY

The present paper is based almost wholly upon the collections at the New York Botanical Garden and the U. S. National Museum, indicated respectively by the letters N. Y. and U. S., and we regret that there has been no opportunity for including a study of material in other herbaria.[1] However, at one or both of these institutions are deposited complete sets of the collections made by North American botanists and nearly complete sets of the collectors resident in Colombia. In addition, there are numerous specimens of the Lehmann, Triana, André, Hartweg and Dawe collections. We are indebted to Sir Arthur Hill, Director of the Royal

[1] After this paper was in proof I examined the collections of Mimosaceæ and Cæsalpiniaceæ in several European herbaria. Additional information resulting from these studies either has been incorporated in the text or has been brought together in an addendum (pp. 192-193). E. P. K.

Botanical Gardens, Kew, and Dr. H. Harms of the Botanisches Museum, Berlin, for special information regarding other collections.

Bentham's numerous papers on Mimosaceæ and Cæsalpiniaceæ, especially his monograph of the Mimoseæ [2] and of *Cassia*,[3] and Micheli's reports on the André [4] and the Lehmann Leguminosæ,[5] have been relied upon for data. Not infrequently localities given by Bentham as being in Colombia actually are in Venezuela; such species have been omitted from the formal list. We suspect that in other cases in which merely "Colombia" is cited by Bentham the specimen really came from some other country, but not having the sheet with full locality data at hand, we have included the species.

We have omitted reference to the numerous species given by Cortés in his monograph [6] of the Colombian Leguminosæ, which constitutes a part of his Flora de Colombia. Much of this valuable work is given over to the medicinal and industrial uses of the plants and to an index of the common names. The family Leguminosæ is the only one actually treated in detail, there being given a list of species, with common names and notes as to geographic distribution. The sources of information for this work are not apparent; the author may have had access to unpublished manuscripts of Triana's or he may have consulted the collections in the herbarium of the Muséum d'Histoire Naturelle at Paris, for many Triana, Goudot, Schlim, Funck and Linden specimens are cited, which, with the exception of Triana's, we have not seen. Many of the species mentioned by Cortés and not treated in the present paper were included by him as a result of misidentification; some are certainly synonyms; others are restricted to Panama, not now within our area. Without doubt some of the species in his Flora should be added to our enumeration, but not having the specimens at hand we have not included any of these questionable species.

Genera of Mimosaceæ in Colombia

Key to Genera

A. Calyx-lobes valvate.
  1. Filaments partly united into a tube; stamens
     many. (Ingeæ)
    Leaves once-pinnate; legumes indehiscent; un-
      armed trees; leaf-rachis glanduliferous..... 1. Inga.

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[2] Revision of the Suborder Mimoseæ. Trans. Linn. Soc. 30: 335–668. 1875.

[3] Revision of the Genus *Cassia*. Trans Linn. Soc. 27: 503–591. 1871.

[4] Les Legumineuses de l'Ecuador et de la Nouvelle-Grenade de la collection de M. Ed. André. Journ. de Bot. 6: 192–193, 197–206. 1892.

[5] Bot. Jahrb. 16: Beibl. 37: 7–9. 1892.

[6] Flora de Colombia, ed. 1, 24–68. 1897: ed. 2, 24–63. 1919.

Leaves bipinnate. (See *Cojoba*.)
  a. Legume not elastically dehiscent from the
     apex; leaves glanduliferous.
    +Legume fleshy or coriaceous.
     Legume circinnate, flat, fleshy, coriaceous,
       indehiscent; petiole glanduliferous;
       leaflets many .... 2. ENTEROLOBIUM.
     Legume straight, curved, or coiled, at length
       dehiscent.
       †Legume-valves (as far as known) twist-
         ing after dehiscence.
       Stipules spinescent; leaflets few, broad;
         seeds (as far as known) with a
         fleshy aril .... 3. PITHOCELLOBIUM.
       Unarmed trees; seeds (as far as
         known) without a fleshy aril.
         (See *Klugiodendron*.)
         ‡Legume flat or compressed.
         Legume very oblique, deeply cre-
           nate on one margin; bractlets
           large; pinnæ 1 pair; leaflets
           1 pair; seeds arillate....... 4. KLUGIODENDRON.
         Legume not deeply crenate; bract-
           lets none, or very small; leaf-
           lets several pairs.
           Flowers capitate or racemose;
             corolla 5-lobed; leaflets
             obovate to linear, numerous. 5. ABAREMA.
           Flowers long-racemose or long-
             spicate; corolla deeply 5-
             lobed; leaflets few, large. 6. PUNJUBA.
         ‡ Legume subterete, mostly monili-
           form .... 7. COJOBA.
       ††Legume-valves not twisting, or legume
         indehiscent.
       Legume septate between the seeds; un-
         armed trees .... 8. ARTHROSAMANEA.
       Legume not septate between the seeds.
         Inflorescence axillary; legume fleshy,
           compressed, indehiscent or very
           tardily dehiscent.
           Unarmed trees with large leaflets. 9. SAMANEA.
           Trees or shrubs, at least the older
             twigs spiny; leaflets small.... 10. CHLOROLEUCON.
         Inflorescence lateral; legume flat,
           thin, coriaceous; unarmed trees
           with broad leaflets............ 11. ZYGIA.
      ‡ Legume thin or papery, flat, mostly de-
        hiscent.
        Trees or shrubs armed with stipular spines. 12. HAVARDIA.
        Unarmed trees.
          Flowers umbellate; calyx narrowly cam-
            panulate, long .... 13. PSEUDOSAMANEA.
          Flowers capitate, rarely umbellate.
            Calyx narrowly campanulate, long;
              corolla and stamens very long.... 14. MACROSAMANEA.
            Calyx not narrowly campanulate,
              short; corolla relatively short.... 15. ALBIZZIA.
  b. Legume elastically dehiscent from apex:
     leaves eglandular .... 16. CALLIANDRA.

2. Filaments distinct.
    a. Stamens many, more than 10. (ACACIEÆ)
        Margins of the transversely septate legume
            separating .... 17. DUGANDIA.
        Margins of the legume-valves not separating.
            *Legume woody or coriaceous; petiole glan-
                duliferous.
            Legume woody, subterete................ 18. VACHELLIA.
            Legume coriaceous, turgid, or compressed.
                Stipular spines usually very large;
                    legume soon dehiscent; inflorescence
                    (in the Colombian species) spicate. 19. MYRMECODENDRON.
                Stipular spines smaller; legumes tardily
                    dehiscent; inflorescence capitate... 20. POPONAX.
            **Legume thin and flat.
            Flowers short-pedicelled; leaves eglandular. 21. ACACIELLA.
            Flowers sessile; petiole, at least usually,
                glanduliferous .... 22. SENEGALIA.
    b. Stamens 10 or fewer.
        *Anthers without glands. (MIMOSEÆ)
        Margins of the legume-valves persistent; un-
            armed plants.
            Trees or large shrubs; flowers bracteolate. 23. LEUCÆNA.
            Herbs or low shrubs; flowers ebracteolate. 24. DESMANTHUS.
        Margins of the legume-valves ultimately
            separating; plants nearly always prickly,
            the leaves mostly eglandular.
            Legume subterete or subtetragonal...... 25. LEPTOGLOTTIS.
            Legume flat.
                Valves of the legume jointed.......... 26. MIMOSA.
                Valves of the legume continuous...... 27. MIMOSOPSIS.
        **Anthers tipped by glands.
        Seeds with endosperm. (ADENANTHEREÆ)
            Perennial unarmed herbs, some of the
                capitate flowers barren............... 28. NEPTUNIA.
            Trees or shrubs; flower spicate or race-
                mose, all perfect.
                Leaflets narrow, opposite; flowers in
                    slender racemes; branches usually
                    spiny .... 29. NELTUMA.
                Leaflets broad, mostly alternate; flowers
                    spicate; unarmed trees........... 30. STRYPHNODENDRON.
        Seeds without endosperm. (PIPTADENIEÆ)
            Legume not transversely septate; trees or
                shrubs .... 31. PIPTADENIA.
            Legume transversely septate; mostly vines.
                Legume woody; leaves cirrhiferous..... 32. ENTADA.
                Legume coriaceous; leaves ecirrhiferous. 33. ENTADOPSIS.
B. Calyx-lobes imbricated. (PARKIEÆ)
    Trees with bipinnate leaves, the flowers in globose
        heads .... 34. PARKIA.

1. INGA Scop., Introd. 289, 1777.

Type species: *Mimosa Inga* L.

KEY TO SPECIES OF INGA

A. Flowers umbellate, all pedicelled. (HETEROPHYLLÆ).
Flowers glabrous or merely puberulent.
Pedicels as long as the calyx, or a little longer.... 1. *I. Archeri.*

Pedicels much longer than the calyx.
  Calyx about 1 mm. long; leaflets 4–7 cm. long,
    long-acuminate .... 2. *I. heterophylla.*
  Calyx about 4 mm. long; leaflets 9–15 cm. long,
    obtusely short-acuminate.................. 3. *I. Lawranceana.*
Flowers strigose.
  Pedicels much longer than the calyx............. 4. *I. santanderensis.*
  Pedicels shorter than the calyx................ 5. *I. Mutisii.*

B. Flowers capitate, spicate, or racemose.

1. *Species with wingless leaf-rachis.*

a. Flowers glabrous.
  Flowers capitate. (DARIENENSES)............... 6. *I. darienensis.*
  Flowers spicate. (CORUSCANTES)
    Leaflets coriaceous........................... 7. *I. coruscans.*
    Leaflets membranous or chartaceous.
      Spikes 10–15 mm. long...................... 8. *I. microstachya.*
      Spikes 6–8 cm. long........................ 9. *I. Caldasiana.*
b. Corolla strigose or pubescent.
  Leaflets densely pubescent beneath. (BRUNNES-
    CENTES)
    Leaflets rounded, cuspidate................... 10. *I. brunnescens.*
    Leaflets acute or acuminate................... 11. *I. culagana.*
  Leaflets glabrous or puberulent.
    Rachis-glands about 4 mm. in diameter; leaflets
      caudate-acuminate. (CYCLADENIÆ)........ 12. *I. cycladenia.*
    Rachis-glands smaller; leaflets not caudate-
      acuminate.
      Leaflets very large, up to 20 cm. long, the
        upper oblanceolate; flowers short-pubes-
        cent. (RUIZIANÆ)..................... 13. *I. Ruiziana.*
      Leaflets smaller; flowers strigose. (NOBILES)
        Upper leaflets oblanceolate................ 14. *I. oblanceolata.*
        None of the leaflets oblanceolate.
          Corolla slender, about 1 mm. in diameter
            Corolla 10–11 mm. long................ 15. *I. olivacea.*
            Corolla 8.5 mm. long................. 16. *I. gracilior.*
          Corolla stouter.
            Corolla about 6 mm. long.............. 17. *I. punctata.*
            Corolla 8–11 mm. long
              Leaflets ovate to elliptic, glabrate... 18. *I. nobilis.*
              Leaflets lanceolate, acuminate, finely
                pubescent .... 19. *I. popayanensis.*

2. *Leaf-rachis winged or margined.*

a. Rachis-glands sessile or subsessile; legume various.
  †Legume (as far as known), flat or compressed.
    ‡Flowers glabrous. (MARGINATÆ)
      Flowers long-spicate....................... 20. *I. marginata.*
      Flowers capitate........................... 21. *I. goniocalyx.*
    ‡‡Corolla strigose or pubescent.
      §Corolla large, mostly 2–3 cm. long, as far as
        known.
        Legume very large, woody, the margins not
          elevated.
          Leaflets subcoriaceous, obtuse or acute,
            glabrous. (SPECTABILES)............ 22. *I. spectabilis.*
          Leaflets chartaceous, short-acuminate,
            sparingly pubescent above........... 23. *I. Smithii.*

Legume coriaceous or chartaceous, the mar-
　　gins elevated. (PANAMENSES)
　　Rachis winged only below the upper pair
　　　　of leaflets........................... 24. *I. brachyptera.*
　　Rachis winged between all pairs of leaflets.
　　　　Leaflets densely pubescent beneath...... 25. *I. antioquensis.*
　　　　Leaflets glabrous.
　　　　　　Leaflets up to 26 cm. long; rachis about
　　　　　　　　8 cm. long...................... 26. *I. heteroptera.*
　　　　　　Leaflets 16 cm. long, or shorter; rachis
　　　　　　　　3–4 cm. long.......... ..... 27. *I. panamensis.*
§§Corolla small, about 15 mm. long, or shorter.
　　(PILOSIUSCULÆ)
　　Rachis with narrow elevated margins; flowers
　　　　densely spicate........................ 28. *I. titiribiana.*
　　Rachis-wings broader.
　　　　Rachis winged only between the upper pair
　　　　　　of leaflets, or between the two upper
　　　　　　pairs.
　　　　　　Calyx 4 mm. long; leaflets rounded or
　　　　　　　　obtuse .... 29. *I. pamplonæ.*
　　　　　　Calyx 6–7 mm. long; leaflets acute...... 30. *I. chartana.*
　　　　Rachis winged between all the pairs of
　　　　　　leaflets.
　　　　　　Flowers spicate.
　　　　　　　　Leaflets oblong-lanceolate............ 31. *I. densiflora.*
　　　　　　　　Leaflets ovate to ovate-elliptic....... 32. *I. sordida.*
　　　　　　Flowers capitate.
　　　　　　　　Leaves glabrous; corolla about 6 mm.
　　　　　　　　　　long .... 33. *I. Bolivariana.*
　　　　　　　　Leaves and twigs pilose or pubescent.
　　　　　　　　　　Upper leaflets oblanceolate; corolla
　　　　　　　　　　　　6.5–7.5 mm. long............... 34. *I. Langlassei.*
　　　　　　　　　　Leaflets all oblong-lanceolate; corolla
　　　　　　　　　　　　11–12 mm. long............... 35. *I. microdonta.*
††Legume (as far as known) slender, terete or
　　subterete, and longitudinally ribbed or striate,
　　or with much-thickened margins. (INGÆ)
Calyx 4–7 mm. long, or shorter; flowers slender.
　　Leaflets rounded or obtuse................... 36. *I. Œrstediana.*
　　Leaflets acute or acuminate.
　　　　Legume subterete, 30 cm. long or longer; leaf-
　　　　　　lets acute or gradually acuminate....... 37. *I. edulis.*
　　　　Legume shorter, its margins less dilated;
　　　　　　leaflets abruptly acuminate............ 38. *I. scabriuscula.*
Calyx more than 8 mm. long; flowers usually
　　stouter.
　　Flowers more or less pedicellate.
　　　　Calyx less than 1 cm. long................. 39. *I. ingoides.*
　　　　Calyx 1 cm. or more long................... 40. *I. spuria.*
　　Flowers sessile.
　　　　‡Flower-buds oblong.
　　　　　　Calyx narrowly tubular, 2–4.5 mm. in
　　　　　　　　diameter.
　　　　　　　　Calyx densely velutinous, 4.5 mm. in
　　　　　　　　　　diameter; corolla 2 cm. long........ 41. *I. Ursi.*
　　　　　　　　Calyx sparingly pubescent, 2 mm. in
　　　　　　　　　　diameter; corolla 3 cm. long...... 42. *I. Chardonii.*

Calyx broadly tubular or subcampanulate, stouter.
§Legume compressed, twice as wide as thick .... 43. *I. eriocarpoides.*
§§Legume terete or subterete.
Calyx teeth triangular-ovate, as broad as long; legume stout, up to 20 mm. thick; stamens about 2.5 cm. long................. 44. *I. fredoniana.*
Calyx teeth ovate-lanceolate: legume very slender, 4–6 mm. thick.
Leaflets 4 or 5 pairs, obtuse or subacute, apiculate, densely tomentose beneath; calyx 8–12 mm. long.................. 45. *I. pseudospuria.*
Leaflets 6–8 (rarely 5) pairs, long acuminate, hirsutulous beneath; calyx more than 12 mm. long .... 46. *I. chinacotana.*
‡‡Flower-buds globose.
Leaflets sessile, the veins not impressed; rachis-glands sessile .... 47. *I. Holtonii.*
Leaflets short-stalked; the veins impressed above; rachis-glands subsessile...... 48. *I. codonantha.*
b. Rachis-glands stipitate; legume broad, compressed, densely tomentose or velutinous. (VULPINÆ)
Rachis-glands slender, elongated.
Calyx glabrous or very nearly so.............. 49. *I. venosa.*
Calyx hirsute or pilose.
Calyx 2–2.5 cm. long....................... 50. *I. fastuosa.*
Calyx 1.5 cm. long.......................... 51. *I. villosissima.*
Rachis-glands stout, short-stipitate............... 52. *I. sierræ.*
Doubtfully of this relationship.................. 53. *I. pseudofastuosa.*

1. Inga Archeri Britton & Killip, sp. nov.

Frutex vel arbor parvus, ramulis puberulis, mox glabris; foliola 1–2-juga, oblonga vel obovata, glabra, abrupte acute vel obtusa, rachide exalata, glandulis parvis, orbiculatis; capitula multiflora, floribus glabris, pedicellis calyci subæqualibus; calycis dentes breves et lati; corollæ lobi ovati, acuti; stamina ad medium conjuncta; legumen lineare, ca. 8–spermum, seminibus elevatis.

Shrub or small tree, about 2 m. high, the twigs puberulent when young, soon glabrous. Petioles about 1 cm. long; leaflets 1 or 2 pairs, oblong or obovate, chartaceous, glabrous, strongly pinnately veined, 3–7 cm. long, abruptly acute or obtuse; rachis wingless, the small glands orbicular; peduncles slender, 2.5–3 cm. long; heads many-flowered, all the flowers glabrous, on pedicels about 1.5 mm. long; calyx 1.5 mm. long, its teeth short and broad; corolla about 5 mm. long, its ovate teeth acute; stamens about 13 mm. long, united to about the middle; young legumes linear, flat, scurfy, stipitate, about 10 cm. long, 10–15 mm. wide, 2–6 together at the end of the fruiting peduncle; mature legume (unattached), about 12 cm. long, 2.5 cm. wide, about 8-seeded, the seeds elevated.

Santa Elena, Antioquia, Colombia, 1500-2000 m. altitude, January 1, 1931, *W. A. Archer 1294*, type (N.Y.).

2. Inga heterophylla Willd. Sp. Pl. 4: 1020. 1806.

Type locality: Pará, Brazil.
Río Carare, *Dawe 420.* Antioquia, *Jervise.* Barranca Bermeja, *Wier 70.* Trinidad; Guiana; Brazil; Bolivia; Peru.

3. **Inga Lawranceana** Britton & Killip, Phytologia 1: 23. 1933.

Type locality: Chapón region, Boyacá, Colombia.
Chapón region, Boyacá, *Lawrance 260* (type). Without locality, *Mutis 1018, 4921.*

4. **Inga santanderensis** Britton & Killip, sp. nov.

Arbor, ramis divaricatis, ramulis, petiolis, folii rachide pedunculisque dense brevipubescentibus; foliola 2–3–juga, chartacea, in veniis subtus pubescentia, suprema obovata vel oblanceolata, cetera oblique oblonga; capitula pluria in panicula parva, pedicellis subfiliformibus, pilosis, calyce multo longioribus; calyx auguste campanulatus, appresso-pubescens, dentibus ovatis; corolla longe strigosa, lobis lanceolatis; stamina infra medium conjuncta.

A tree, 2.5–4 m. high, with slender divaricate branches, the twigs, petioles, leaf-rachis and peduncles densely short-pubescent. Petiole and leaf-rachis 5–7 cm. long; leaflets 2 or 3 pairs, chartaceous, pubescent on the prominent veins beneath and strongly reticulate-veined, the apex acute, the base narrowed; upper pair of leaflets obovate or oblanceolate, about 12 cm. long and 5–6 cm. wide, the second pair obliquely oblong, about 10 cm. long, or shorter; heads several in a small panicle; peduncles 2–4 cm. long; flowers several, all on nearly filiform, pilose pedicels 10–13 mm. long; calyx narrowly campanulate, appressed-pubescent, 4 mm. long, its ovate teeth acute; corolla long-strigose, about 9 mm. long, its lobes lanceolate; stamens about 17 mm. long, united below the middle.

Open hillside, between Piedecuesta and Las Vegas, Santander, Colombia, 2000–2100 m. altitude, December 19, 1926, *Killip & Smith 15477*, type (N.Y.). Ocaña, Norte de Santander, *Schlim 204* (recorded by Bentham as *I. quaternata* Poepp. & Endl.). GUAMO, applied to many species of *Inga*.

5. **Inga Mutisii** Britton & Killip, sp. nov.

Ramuli sparse brevipubescentes; foliola 3–juga, rachide exalata, glabra, glandulis orbiculatis sessilibus, coriacea, nitidula, supra glabra, subtus sparsissime pilosula, apice abrupte breviter acuminata, suprema oblanceolata, inferiora oblonga; inflorescentia dense puberula vel brevipubescens, capitulis paniculatis, multifloris, pedicellis pilosis, calyce brevioribus; calyx et corolla dense strigosa, dentibus ovato-lanceolatis.

Twigs sparingly short-pubescent. Petiole and leaf-rachis glabrate, wingless, about 11 cm. long, rather stout, the glands orbicular, sessile; leaflets 3 pairs, coriaceous, sublustrous, glabrous above, sparingly or densely pilosulous beneath, abruptly short-acuminate at apex, cuneate at base, the terminal pair oblanceolate or oblong, 15–22 cm. long, 7–9 cm. wide, the lower oblong, 12–13 cm. long, 4.5–5 cm. wide; inflorescence densely puberulent or short-pubescent, the panicle of heads about 15 cm. long; peduncles 2–3 cm. long; umbels many-flowered, the pedicels pilose, 2–3 mm. long; calyx densely strigose, 5 mm. long, its teeth ovate-lanceolate, acute; corolla densely strigose, 6 mm. long, with ovate-lanceolate acute lobes; stamen-tube about as long as the corolla, or somewhat longer.

Colombia, 1760–1808, *Mutis 3644*, type (U.S.). Chiquinquirá, Cundinamarca, *Ariste Joseph B. 126.*

6. **Inga darienensis** Seem. Bot. Voy. Herald, 117, *pl. 23.* 1853.

Type locality: Cape Corrientes, Colombia.
Cape Corrientes, *Seemann 1050* (type).

7. **Inga coruscans** H. & B.; Willd. Sp. Pl. 4: 1017. 1806.

Mimosa coruscans Poir. in Lam. Encycl. Suppl. 1: 43. 1810.

Type locality: South America.
Neiva, Huila, *Pennell 970.* Río Viejo, *Humbodt & Bonpland* (co-type). British Guiana.

8. Inga microstachya Britton & Killip, sp. nov.

Glabra, floribus exceptis; rachis et petiolus teretia, rachide exalata, glandulis concavis; foliola 4–5–juga, oblongo-lanceolata, chartacea, acuminata; inflorescentia brevispicata, spicis tenuipedunculatis, 4–7–fasciculatis, 10–15 mm. longis; calyx rufo-puberulus; corolla ad basim glabra, supra puberula.

Plant, except flowers, essentially glabrous throughout. Rachis and petiole 8–12 cm. long, terete, slender, the rachis wingless, its glands concave, sessile; leaflets 4 or 5 pairs, chartaceous, lustrous, oblong-lanceolate, acuminate at apex, rounded or subacute at base, subsessile, the terminal pair about 13 cm. long and 4 cm. wide, the lowest pair 5 cm. long, 2 cm. wide; inflorescence short-spicate, the spikes slender-peduncled, in fascicles of 4–7, 10–15 mm. long, 8–10 mm. wide; calyx 1–1.5 mm. long, rufo-puberulent, the teeth triangular; corolla glabrous toward base, puberulent above, 4–6 mm. long, its lobes lanceolate.

Colombia, 1760–1808, *Mutis 445, 3633*, type (U.S.), *7537*.

9. Inga Caldasiana Britton & Killip, sp. nov.

Glabra, inflorescentiæ ramulis sparse pilosulis; rachis et petiolus teretia, rachide exalata, glandulis orbiculatis, concavis; foliola 3–juga, chartacea, suprema elliptica vel subobovata, cetera oblongo-lanceolata vel elliptico-lanceolata; flores in spicis 6–8 cm. longis; calyx minimus, globoso-campanulatus; corolla infundibularis, lobis triangulato-ovatis.

Plant nearly glabrous throughout, the inflorescence-branches sparingly pilosulous. Rachis and petiole 6–9 cm. long, terete, slender, the rachis wingless, its glands orbicular, concave, about 2 mm. in diameter; leaflets 3 pairs, chartaceous, acuminate to obtuse, the terminal pair elliptic or slightly obovate, 8–15 cm. long and 4–7 cm. wide, the others oblong-lanceolate or elliptic-lanceolate, the lowest 4–6 cm. long and 2 cm. wide; flowers in slender spikes 6–8 cm. long, including peduncle: calyx very small, globose-campanulate, 0.7–0.8 mm. long, the teeth minute; corolla funnelshaped, glabrous, about 5 mm. long, the lower half much narrowed, the lobes triangular-ovate, acute; stamens about 7 mm. long.

Colombia, 1760–1808, *Mutis 3539*, type (U.S.), *443, 446, 3541*.

10. Inga brunnescens Britton & Kilip, sp. nov.

Rufo-tomentosa; rachis exalata, glandulis orbiculatis, concavis; foliola 6–juga, apice rotunda et cuspidata, coriacea, subtus rufo-hirsuta, suprema obovata, cetera oblonga; inflorescentia paniculiformis, spicis geminatis; calycis dentes late triangulares; corolla dense appresso-strigosa; stamina per ¾ longitudinis conjuncta.

Twigs, leaf-rachis and branches of inflorescence densely rufo-tomentose. Petiole and rachis 30–35 cm. long, the rachis wingless, its glands orbicular, concave, sessile; leaflets 6 pairs, rounded and cuspidate at apex, rounded at base, with the petiolules stout, up to 5 mm. long, coriaceous, rufo-tomentose on nerves, lustrous and subglabrous above, rufo-hirsute beneath, the terminal pair obovate, up to 15 cm. long and 7 cm. wide, the lower pairs oblong, decreasing to 6 cm. long, 3 cm. wide: inflorescence paniculiform, the spikes in pairs, the flowering portion up to 3.5 cm. long; calyx rufo-tomentose, about 4 mm. long, the teeth broadly triangular, acute, about 1 mm. long; corolla about 15 mm. long, densely appressed-strigose, its lobes lanceolate, acute; stamens about 2 cm. long, united to upper quarter.

Colombia, 1760–1808, *Mutis 3523*, type (U.S.), *444*.

11. Inga culagana Britton & Killip, sp. nov.

Arbor, ramulis et pedunculis dense puberulis; foliola 3–4–juga, acuta, subtus pilosa, suprema obovata, cetera elliptica vel ovato-elliptica, rachide

exalata, dense puberula; flores breviter spicati, sessiles; calyx dense puberulus, dentibus lanceolatis, obtusis; corolla strigosa, lobis lanceolatis, acutis; stamina infra medium conjuncta; legumen quadrangulatum, dense velutinum.

A tree, 8–10 m. high, the twigs, leaf-rachis and peduncles densely puberulent. Petiole and rachis 8–15 cm. long; rachis wingless, its glands, if any, obscure; leaflets 3 or 4 pairs, chartaceous, acute, densely short-pubescent, becoming glabrous above, densely short-pilose beneath, and strongly pinnately veined, the terminal pair obovate, 10–20 cm. long, the others elliptic or ovate-elliptic, smaller; peduncle about 3 cm. long; flowers several, sessile, short-spicate; calyx densely puberulent, 6–7 mm. long, its ovate teeth obtuse; corolla 12–13 mm. long, strigose, its lobes lanceolate, acute; stamens about 2 cm. long, united below the middle; young legume slender, subterete, twisted, longitudinally ribbed, about 10 cm. long, about 6 mm. in diameter, densely short-pubescent; older legumes nearly equally 4-sided, and 4-angled, 26 cm. long, 15–18 mm. broad, densely velutinous, pointed.

Culagá Valley, near Tapatá, Norte de Santander, Colombia, 2100 m. altitude, March 4, 1927, *Killip & Smith 20165*, type (N.Y.). Sonsón, Antioquia, *Archer 655*, fruiting specimen. Without locality, *Mutis 3524, 4367*. GUAMO CHURIMO

12. Inga cycladenia Pittier, Contr. U. S. Nat. Herb. 18: 184. 1916.

Type locality: Micay-Sajja and Timbiquí, Colombia.
Timbiquí, El Cauca, *Lehmann B. T. 662* (type). Endemic.

13. Inga Ruiziana G. Don. Gen. Syst. 2: 391. 1832.

Type locality: Peru.
Río Timbiquí, El Cauca, *Lehmann 8986* (type). Mocoa, Caquetá, *Sprague 408*. Peru; Brazil.

14. Inga oblanceolata Britton & Killip, sp. nov.

Foliola 3–5-juga, rachide exalata, foliolis chartaceis, in nerviis supra pulverulentis subtus sparse pilosulis, acuminatis vel acutis, supremis anguste oblanceolatis, ceteris anguste oblongo-lanceolatis; inflorescentia paniculiformis, floribus in capitulis densis, dense hirsuti; calyx tubuloso-campanulatus, lobis triangulari-ovatis; corolla infundibularis, lobis lanceolatis; stamina ad 2/3 longitudinis conjuncta.

Rachis and petiole slender, 11–14 cm. long, wingless, the glands orbicular, flattened. Leaflets 3–5 pairs, chartaceous, finely pulverulent on nerves above, very sparingly pilosulous on nerves beneath, otherwise glabrous, abruptly or gradually acuminate, and mucronulate at apex, narrowed at base, short-petioluled, the terminal pair narrowly oblanceolate, 7–13 cm. long. 1–4 cm. wide, the lateral pairs narrowly oblong-lanceolate, the lowest pair about 4 cm. long and 1.3 cm. wide; inflorescence paniculiform, the branches flavo-tomentose, the flowers in dense clusters about 1.5 cm. wide; bracts soon deciduous; calyx tubular-campanulate, about 4 mm. long, 2.5 mm. wide at throat, densely hirsute, its lobes triangular-ovate; corolla funnelshaped, about 8 mm. long, densely hirsute, its lobes lanceolate, acute; stamens 1–1.2 cm. long, united about to upper third.

Colombia, 1760–1808, *Mutis 3635*, type (U.S.). Isla brava, Río Magdalena, *Andre 364*. Near Fusagasugá, Cundinamarca, *Andre 1939*.

15. Inga olivacea Sprague, Trans. & Proc. Bot. Soc. Edinb. 22: 430. 1904.

Type locality: Between Villavicencio and Bogotá, Colombia.
Between Villavicencio and Bogotá, *Sprague* (type). Umbría, Putumayo, *Klug 1737*. Lands of Loba, Bolívar, *Curran 119*, fruiting specimen.

16. Inga gracilior Sprague, Trans. & Proc. Bot. Soc. Edinb. 22: 431. 1904.

Type locality: Mocoa, Caquetá, Colombia.
Mocoa, Caquetá, *Sprague 365* (type).

17. Inga punctata Willd. Sp. Pl. 4: 1016. 1806.

Type locality: Caracas, Venezuela.
Frequent in Colombia. Venezuela; Trinidad; Tobago; Surinam; Panama to Guatemala.

18. Inga nobilis Willd. Enum. Hort. Berol. 1047. 1809.

Inga Humboldtiana H. B. K. Nov. Gen. & Sp. 6: 285. 1824.

Type locality: Brazil.
Cundai, Cundinamarca, *Triana 4461.* Dept. Bolívar, *Pennell 4162.* Río Viejo, Bolívar, *Humboldt & Bonpland* (type of *I. Humboldtiana*). Lake Sapatoza, *Allen 200.* Venezuela to French Guiana and Brazil. GUAMITO.

19. Inga popayanensis Pittier, Contr. U. S. Nat. Herb. 18: 185. 1916.

Type locality: Highlands of Popayán, Colombia.
Popayán, *Lehmann 829, 5751* (type), *7808.* Cuatro Esquinas, El Cauca, *Pennell & Killip 6340.* ?Puerto Wilches, Santander, *Killip & Smith 14935* (young fruit). Bogotá, *Triana 4469.* Medellín, *Toro 27?.*

20. Inga marginata Willd. Sp. Pl. 4: 1015. 1806.

?Inga sapida H. B. K. Nov. Gen. & Sp. 6: 286. 1823.

Type locality: Caracas, Venezuela.
Frequent at middle altitudes in Colombia. Ecuador; Peru; Bolivia; Venezuela; Brazil; Panama to Costa Rica. GUAMO CHURIMO, GUAMO NEGRITO.

21. Inga goniocalyx Britton & Killip, sp. nov.

Glabra; petiolus et rachis anguste alata, glandulis breviter cylindricis; foliola 3–juga, subcoriacea, reticulata, obtuse acuminata, suprema elliptica vel ovato-elliptica, cetera oblonga, nonnumquam obliqua; inflorescentia capitata, pauciflora; calyx 5–angulatus, tubuloso-campanulatus, dentibus triangularibus; corolla cylindrica, lobis anguste lanceolatis.

Plant glabrous throughout. Rachis and petiole 5–7 cm. long, narrowly winged and glanduliferous between each pair of leaflets, the upper pair of wings 2.5–3.5 cm. long, about 2 mm. wide, the glands short-cylindric; leaflets 3 pairs, subcoriaceous, lustrous, rather prominently reticulate-veined, obtusely acuminate at apex, narrowed to a rounded base, subsessile, the terminal pair elliptic or ovato-elliptic, 12–18 cm. long, 5–9 cm. wide, the others oblong, sometimes oblique, the lower about 6 cm. long, 3 cm. wide; inflorescense capitate, few-flowered, the peduncle slender, 2–5 cm. long, the flowers sessile; calyx 5–angled, tubular-campanulate, 2–3 mm. long, its teeth triangular, subacute; corolla cylindric, 7–8 mm. long, very slightly enlarged at apex, its lobes narrowly lanceolate, about 1 mm. long.

Colombia, 1760–1808, *Mutis 4927,* type (U.S.), *1967.*

22. Inga spectabilis (Vahl) Willd. Sp. Pl. 4: 1017. 1806.

Mimosa spectabilis Vahl, Skr. Nat. Selsk. Kjob. 2¹: 219, *pl. 10.* 1792.
Inga fulgens Kunth, Mim. 36, *pl. 11.* 1819.
Inga lucida H. B. K. Nov. Gen. & Sp. 6: 287. 1824.

Type locality: Santa Marta, Colombia.
Bolívar, *Curran 147, 175a.* Boyacá, *Lawrance 57.* Antioquia, *Toro 453; Chardon 133; Archer 1428, 1880, 2035.* Timbiquí, El Cauca, *Lehmann B. T. 686.* Ecuador; Panama; Costa Rica. GUAMO MACHETO.

23. Inga Smithii Britton, sp. nov.

Rachis foliorum crassa, glabra, infra jugum supremum foliolorum anguste alata, glandulis concavis, orbiculatis; foliola 2–3–juga, chartacea, reticulata, sparse hirsutula, nitidula, late elliptica vel ovato-elliptica, breviter acuminata; legumen late lineare, lignosum, sessile, rugulosum.

Leaf-rachis stout, glabrate, narrowly winged below the upper pair of leaflets, the concave glands orbicular. Leaflets 2 or 3 pairs, chartaceous,

strongly veined, coarsely reticulate, faintly lustrous, bearing short scattered hairs on both surfaces, broadly elliptic to ovate-elliptic, 12–18 cm. long, 7–11 cm. wide. the apex abruptly short-acuminate, obliquely obtuse; legume broadly linear, woody, sessile, flat, rugulose, 30–38 cm. long, 6–7 cm. wide, the margins about 12 mm. thick.

Polonia, near Puerto Wilches, Santander, Colombia, 100 m. altitude, December 1, 1926, *Killip & Smith 14933*, type (N.Y.).

24. Inga brachyptera Benth. Lond. Journ. Bot. 4: 610. 1845.

Type locality : Tumaco, Colombia
Known only from the type locality, in the Department of Nariño ; the type, collected by Hinds, seen at Kew.

25. Inga antioquensis Britton & Killip, sp. nov.

Rachis foliorum late alata, glandula orbiculata, parva, inter jugum quodque foliolorum; foliola 2–3-juga. chartacea, late ovata vel elliptica, obtusa vel obtuse subacuta, ad basim rotundata vel subcordata, supra glabra, subtus dense pubescentia ; legumen oblongum, sessile, compressum, coriaceum, glabrum.

Leaf-rachis broadly winged, with a small orbicular gland between each pair of leaflets. Leaflets 2 or 3 pairs, chartaceous, broadly ovate or elliptic, obtuse or bluntly acutish at apex, rounded or slightly subcordate at base, glabrous and faintly veined above, short-pubescent beneath, the larger ones about 14 cm. long and 8 cm. wide ; legume oblong, sessile, compressed, coriaceous, glabrous, 10–14 cm. long, 2.5–4 cm. wide and 6 mm. thick, with broad, slightly elevated margins.

Loreto, vicinity of Medellín, Colombia, December 21, 1927, *Toro 858*, type (N Y.) Mompos Island, Bolívar, *Curran 226*.

26. Inga heteroptera Benth. Lond. Journ. Bot. 4: 611. 1845.

Type locality : San Pedro, Colombia.
Known only from the type locality ; the type, collected by Hinds, seen at Kew

27. Inga panamensis Seem. Bot. Voy. Herald 117. 1853.

Type locality : Near Cruces, Panama.
Colombia *(Linden 366,* according to Bentham). Panama. Schlim's 256, from Ocaña, Norte de Santander, is doubtfully referred here by Bentham.

28. Inga titiribiana Britton & Killip, sp. nov.

Ramuli inflorescentia foliorum rachisque dense rufo-hirsuta, rachide anguste marginata inter jugum quodque foliolorum, glandula orbiculata; foliola 6-juga, chartacea, glabra, supra lucentia, subtus pallidiora et in veniis pubescentia, suprema oblanceolata, cetera oblonga vel oblongo-lanceolata ; flores dense spicati ; calyx laxe strigosi, dentibus ovatis; corolla dense strigosa, lobis ovatis ; stamina ultra medium conjuncta.

Twigs, inflorescence and leaf-rachis densely rufo-hirsute. Leaves short-petioled, the narrowly margined rachis bearing an orbicular gland between each pair of leaflets ; leaflets 6 pairs, chartaceous, acute or acutish at the apex, rounded at the base, pinnately and reticulate-veined, glabrous, lustrous and dark green above, paler beneath, and pubescent on the veins, the upper pair obovate. about 12 cm. long and 6 cm. wide, the others oblong or oblong-lanceolate, 5–11 cm. long; flowers in dense peduncled spikes 3–6 cm. long, the peduncles about as long or somewhat longer; bractlets linear, about 3 mm. long; calyx about 4 mm. long, loosely strigose, its teeth ovate, acute ; corolla about 8 mm. long, densely strigose, its teeth ovate, acute ; stamens about 15 mm. long, united to above the middle.

Titiribí, vicinity of Medellín, Antioquia, Colombia, September 4, 1927, *Toro 524*, type (N. Y.) ; *Chardon 134.*

29. Inga pamplonæ Britton & Killip, sp. nov.

Arbor, ramulis foliis inflorescentiaque dense tomentulosis; rachis solum infra jugum supremum foliolorum alata, glandulis inconspicuis; foliola 2–3–juga, elliptica, rotunda vel obtusa; flores brevispicati; calyx campanulatus, dentibus ovatis, acutis; corollæ lobi oblongi, acuti; stamina ultra medium conjuncta.

A tree, 5–8 m. high, the twigs, foliage and inflorescence densely tomentulose. Leaves short, the rachis narrowly expanded into a small wing below the upper pair of leaflets only, the glands inconspicuous; leaflets 2 or 3 pairs, nearly elliptic, rather strongly veined, rounded or obtuse at both ends, 5–10 cm. long, 2.5–6 cm. wide; peduncles 1–3 cm. long; flowers short-spicate; calyx campanulate, 4 mm. long, densely appressed-pubescent, its ovate teeth acute; corolla about 10 mm. long, densely strigose, its oblong lobes acute; stamens about 15 mm. long, united to above the middle.

Open hillside, vicinity of Pamplona, Norte de Santander, Colombia, 2300–2400 m. altitude, February 27, 1927, *Killip & Smith 19777*, type (N.Y.).

30. Inga chartana Britton & Killip, sp. nov.

Arbor, ramulis foliorum rachide inflorescentiaque dense brunneo-puberulis; rachis infra juga duo suprema foliolorum alata, glandulis orbiculatis inter jugum quodque; foliola 3–4–juga, chartacea, acuta, supra dense puberula, subtus brevipubescentia, suprema obovata, cetera ovato-lanceolata vel oblonga; flores dense spicati; calyx tubuloso-campanulatus, dentibus ovatis, acutis; stamina ultra medium conjuncta.

A tree, 8–12 m. high, the stout twigs, the leaf-rachis and the inflorescence densely brown-puberulent. Petiole and rachis about 12 cm. long, or shorter; glands orbicular, concave, borne at each pair of leaflets: rachis with a wing 1.5–2 cm. long and 4–6 mm. wide below the upper pair of leaflets, and a much smaller one below the next pair; leaflets 3 or 4 pairs, chartaceous, 7–12 cm. long, acute, the base rounded or obtuse, densely puberulent above and short-pubescent beneath, the upper pair obovate, the others ovate-lanceolate to oblong; flowers densely spicate, the spikes about 2 cm. long, on peduncles about as long, or somewhat longer; calyx tubular-campanulate, densely short-pubescent, 6–7 mm. long, its ovate teeth acute; corolla about 11 mm. long, strigose, its teeth acute; stamens about 15 mm. long, united to a little above the middle.

Open hillside, vicinity of Charta, Santander, Colombia, 2000–2400 m. altitude, February 9, 1927, *Killip & Smith 19088*, type (N.Y.).

31. Inga densiflora Benth. Trans. Linn. Soc. 30: 617. 1875.

Type locality : Near Tarapoto, Peru
Ibagué, *Triana*. Falcón, *André 3615*. Dept. Antioquia, *Archer 593, 654, 658 ; Chardon 148*. Peru. (Illustrated by Pittier, Contr. U. S. Nat. Herb. 18: *pl. 97.*). GUAMO MACHINTO.

32. Inga sordida Pittier, Contr. U. S. Nat. Herb. 18: 191. 1916.

Type locality : Popayán, Cauca, Colombia.
Popayán, *Lehmann 904* (type). Endemic.

33. Inga Bolivariana Britton & Killip, sp. nov.

Glabra, inflorescentia excepta; rachis anguste alata, glandulis orbiculatis, concavis; foliola 3–4–juga, ovato-oblonga, subcoriacea, abrupte cuspidato-acuminata; inflorescentia capitata; calyx tubuloso-campanulatus, lobis parvis, rotundis, sparse pilosulis; corolla appresso-rufo-hirsuta, lobis lanceolatis; stamina ad ¾ longitudinis conjuncta.

Plant glabrous throughout except inflorescence. Rachis and petiole 8–12 cm. long, the rachis narrowly winged between each pair of leaflets, the wings 2–2.5 mm. wide, the glands orbicular, concave, sessile, borne between each pair of leaflets; leaflets 3 or 4 pairs, ovate-oblong, subcoriaceous, prominently nerved,

abruptly cuspidate-acuminate at apex, narrowed at base, the terminal pair up to 16 cm. long and 7.5 cm. wide, the lower pairs 11–13 cm. long, 5–5.5 cm. wide, oblique; bracts spatulate, about 8 mm. long, persistent; inflorescence capitate, about 1 cm. wide, the peduncles slender, 2–2.5 cm. long; flowers sessile; calyx tubular-campanulate, 2.5–3 mm. long, sparingly pilosulous on the small rounded lobes; corolla about 6 mm. long, appressed-rufo-hirsute, its lobes lanceolate, acute; stamens 10 mm. long, united up to upper quarter.

Colombia, 1760–1808, *Mutis 3636*, type (U.S.), 3642.

This species is named in honor of Dr. Ignacio Bolívar, Director of the National Academy of Sciences, Madrid, to whom the botanical world is largely indebted for the re-examination of the historic Mutis herbarium.

34. Inga Langlassei Pittier, Contr. U. S. Nat. Herb. 18: 189. 1916.

Type locality: Western Cordillera, Cauca Valley.
Cauca Valley, El Valle, *Langlassé 63* (type). Endemic.

35. Inga microdonta Britton & Killip, sp. nov.

Ramuli dense rufo-tomentulosi; rachis anguste alata, glandulis sessilibus; foliola 4-juga, oblongo-lanceolata, acuminata, supra in costa rufo-hirtella, subtus appresso-rufo-hirsuta; flores dense capitati; calyx tubulosus, dentibus minutis; corolla strigosa, lobis triangulato-lanceolatis; stamina ultra medium conjuncta.

Twigs densely rufo-tomentulose. Petiole and leaf-rachis rufo-hirtellous, the rachis 12–15 cm. long, bearing between each pair of leaflets a sessile concave gland about 2 mm. in diameter, narrowly winged, the wings up to 2 mm. wide; leaflets 4 pairs, oblong-lanceolate acuminate, rounded at base, above lustrous, densely rufo-hirtellous on midnerve, sparingly so elsewhere, beneath appressed-rufo-hirsute, the terminal pair 13 cm. long, 5 cm. wide, the lowest pair 5 cm. long, 2 cm. wide; peduncles 3–3.5 cm. long; flowers densely capitate, the heads 2–2.5 cm. long, up to 4 cm. wide; calyx tubular, about 3 mm. long, very sparingly appressed-hirsutulous, the teeth minute; corolla 11–12 mm. long, strigose, the lobes triangular-lanceolate, about 3 mm. long; stamens about 40, 15 mm. long, united to a little above the middle.

Colombia, 1760–1808. *Mutis 3526,* type (U.S.), 3638.

Distinguished from *I. Langlassei* by longer corolla tube, leaves not emarginate at base or long-apiculate at apex, not oblanceolate, and scarcely falcate.

36. Inga Œrstediana Benth.; Seem. Bot. Voy. Herald 117. 1853.

Type locality; Panama.
Pasca, Cundinamarca, *Triana 4467*. Bogotá, *Ariste Joseph B. 121*. Medellín, *Toro 1075*. Río Sucio, El Cauca, *Pennell & Killip 8133*. Venezuela; Panama; Costa Rica.

37. Inga edulis Mart. Flora 20: Beibl. 113. 1837.

Type locality: Brazil.
Mutis 3647. Santa Marta, *H. H. Smith 27*. Medellín, *Toro 1336*. Ibagué, *Triana 4466*. Venezuela to Surinam, Peru and Brazil; Trinidad; Grenada; Panama to Veracruz. GUAMO RABO DE MONO, GUAMO SANTAFDRDÑO.

38. Inga scabriuscula Benth. Lond. Journ. Bot. 4: 606. 1845.

Type locality: Surinam.
Colombia (according to Bentham). Surinam; Brazil.

39. Inga ingoides (Rich.) Willd. Sp. Pl. 4: 1012. 1806.

Mimosa ingoides Rich. Act. Soc. Hist. Nat. Paris 1: 113. 1792.
Inga ornata Kunth, Mim. 46, pl. 14. 1819.

Type locality: Cayenne.
Río Sinú, Bolívar, *Pennell 4701*. Río Frío, Magdalena, *Walker 1215*. Río Dedo, Caquetá, *Uribe*. Venezuela to French Guiana; Guadeloupe; Dominica; Martinique; Trinidad.

40. Inga spuria Willd. Sp. Pl. 4: 1011. 1806.

?Inga Berteriana DC. Prodr. 2: 434. 1825.

Type locality: Venezuela (Cumaná, see Kunth, Mim. *pl. 12*).
Common in Colombia. GUAMO ARROYERO, GUAMO CHURIMO, GUAMO MACHO.

41. Inga Ursi Pittier, Contr. U. S. Nat. Herb. 18: 215. 1916.

Type locality: Colombia.
Popayán, *Lehmann 5750* (type). Endemic.

42. Inga Chardonii Britton & Killip, sp. nov.

Rachis foliorum dense brevipilosa, inter juga 1 vel 2 suprema foliolorum alata; foliola 3–4-juga, supra laxe subtus dense brevipilosa, obtusa vel subacuta, suprema obovata, cetera elliptica vel elliptico-lanceolata; flores brevispicati; calyx anguste tubulosus, sparse pubescens, dentibus ovatis, acutis; corolla tenuissime, lobis lanceolatis; stamina ultra medium conjuncta; legumen lineare, subcompressum, dense velutinum.

Rachis of leaves 15–20 cm. long, densely short-pilose, winged between the 1 or 2 upper pairs of leaflets, rarely between the others. Leaflets 3 or 4 pairs, strongly pinnately veined, subchartaceous, 9–15 cm. long, 2.5–8 cm. wide, loosely short-pilose above, densely so beneath, subsessile, obtuse or acutish, the upper pair obovate, the others elliptic to elliptic-lanceolate; flowers short-spicate, the axis about 2 cm. long; calyx narrowly tubular, slender, about 10-ribbed, 9 mm. long, 2–3 mm. in diameter, sparingly loosely pubescent, its ovate teeth acute; corolla very slender, loosely strigose, about 3 cm. long, its lobes lanceolate, acutish; stamens about 5 cm. long, united to above the middle; legume linear, somewhat compressed, densely velutinous, 20–35 cm. long, about 16 mm. wide and 8 mm. thick, with a narrow sunken median area and thickened margins.

Near Fredonia, Antioquia, Colombia, May 27, 1926, *Carlos E. Chardon 135*, type (N. Y.). Venecia, Antioquia, *Chardon 137*. Sonsón, Antioquia, *Archer 657, 659* (fruiting specimens).

43. Inga eriocarpoides Britton & Killip, sp. nov.

Ramuli petioli inflorescentiaque dense brevipubescentia; rachis inter jugum quodque foliolorum late alata, glandulis orbiculatis; foliola 4–5-juga, ovato-oblonga vel ovato-lanceolata, subchartacea, acuta, costa supra pubescente, subtus pilosa; flores spicati, alabastris oblongis; calyx dense brevipubescens; corolla dense et longe strigosa; stamina infra medium conjuncta; legumen lineare, rectum, compressum, dense velutinum, duplo longior quam latior.

Twigs, petioles and inflorescence densely short-pubescent. Leaf-rachis broadly winged between each pair of leaflets, the glands orbicular, concave; leaflets 4 or 5 pairs, ovate-oblong to ovate-lanceolate, subchartaceous, 6–12 cm. long, 2.5–4 cm. wide, the apex acute, the base rounded or obtuse, the upper surface obscurely veined, pubescent on the midvein, otherwise glabrate, the under side delicately veined and reticulated, the midvein pilose; peduncles rather slender, 5–7 cm. long; flowers spicate, the spikes somewhat shorter than the peduncles; buds oblong, obtuse; calyx 12–17 mm. long, densely short-pubescent, its teeth ovate, acute; corolla about 25 mm. long, densely long-strigose, its ovate-lanceolate lobes acute; stamens nearly 5 cm. long, united below the middle; legume linear, straight, compressed, densely velutinous, slightly constricted, short-tipped, about 22 cm. long, 8-10 mm. wide, 3–4 mm. thick.

Vicinity of Medellín, Antioquia, Colombia, March 19, 1926, *Toro 67*, type (N.Y.).

44. Inga fredoniana Britton & Killip, sp. nov.

Ramuli inflorescentiaque dense tomentosa; folii rachis late alata, glandulis inconspicuis; foliola 4–5-juga, chartacea, oblongo-lanceolata vel (suprema) oblongo-obovata, acuta, subtus dense tomentosa; flores pubescentes, in spicis densis brevibus; calyx campanulatus, dentibus brevibus; stamina ultra medium conjuncta; legumen subterete, crassum. dense puberulum, valde pluricostatum.

Twigs, inflorescence and under leaf-surfaces densely tomentose, the upper leaf-surfaces densely short-pubescent. Leaf-rachis broadly winged, bearing an inconspicuous gland between each pair of leaflets; leaves short-petioled: leaflets 4 or 5 pairs, chartaceous, oblong-lanceolate, or the upper pair oblong-obovate, strongly many-veined, acute or acutish, dark green above, pale beneath, 5-9 cm. long; flowers in dense short spikes, the peduncles 2-6 cm. long; bractlets suborbicular, about 2 mm. broad; calyx campanulate, 7 mm. long, densely short-pubescent, its teeth ovate, about 1 mm. long, acute; corolla about 2 cm. long, densely long-pubescent, its lobes oblong-lanceolate, acute; stamens about 2.5 cm. long, united to above the middle; legume subterete, stout, densely puberulent, about 90 cm. long, strongly several-ridged, constricted irregularly, its maximum thickness about 2 cm.

Fredonia, vicinity of Medellín, Antioquia, Colombia, December 20, 1927, *Toro 8¼*, type (N.Y.) Cartago, El Valle, *André 216, in part*.

45. Inga pseudospuria Britton & Killip, sp. nov.

Arbor fere ubique dense rufo-tomentosus; rachis anguste alata, glandulis sessilibus, concavis; foliola 4-5-juga, chartacea, oblongo-lanceolata, oblonga vel (suprema) oblongo-obovata, obtusa vel subacuta, apiculata, supra in venis pubescentia, demum glabrata; flores spicati; calyx dense pubescens; corolla strigosa; legumen terete, elongatum, tenuissimum, tenuiter costatum.

Tree. 5-8 m. high, the twigs, leaf rachis, under surface of leaves, inflorescence and legumes densely rufo-tomentose. Petiole and rachis 10-12 cm. long, the rachis between each pair of leaflets narrowly winged and bearing a sessile concave gland 1-1.5 mm. in diameter; leaflets 4 or 5 pairs, chartaceous, oblong, oblong-lanceolate, or (upper pair) oblong-obovate, 6-12 cm. long, 2-4 cm. wide, obtuse or subacute and apiculate at apex, rounded or obtuse at base, the faintly shining upper surface pubescent on the veins, otherwise glabrate when old; peduncles stout, 1-5 cm. long; flowers in spikes 2-3 cm. long; calyx densely pubescent, 10-12 mm. long, its teeth ovate-lanceolate, acute; corolla strigose, about 20 mm. long, the teeth ovate-lanceolate, acute; stamens about 3.5 cm. long; legume terete, very slender, 15-30 cm. long, only 5-6 mm. in diameter, finely several-ridged.

Open hillside, north of Labateca, Norte de Santander, Colombia, 1480-1550 m. altitude, March 12, 1927, *Killip & Smith 2052¼*, type (N.Y.) Bello, Antioquia, *Toro 726*. Without locality, *Mutis 2255*. RABO DE MONO.

46. Inga chinacotana Britton & Killip, sp. nov.

Arbor, ramulis foliorum rachide inflorescentiaque dense brunneo-tomentosis; rachis inter jugum quodque foliolorum alata, glandulis orbiculatis, concavis; foliola 5-8-juga, chartacea, oblonga vel oblongo-lanceolata, longe acuminata, supra brevipubescentia, subtus hirsutula; flores spicati; calyx subcylindrica, dentibus ovato-lanceolatis; corolla longe strigosa: stamina infra medium conjuncta.

A tree, 8-11 m. high, with densely brown-tomentose twigs, leaf-rachis and inflorescence. Petiole and rachis 10-20 cm. long; rachis winged between each pair of leaflets, and having sessile orbicular concave glands about 1.5 mm. in diameter; leaflets 6-8 (rarely 5) pairs, chartaceous, oblong or oblong-lanceolate, long-acuminate, 3-10 cm. long, 1-4 cm. wide, rather strongly pinnately veined, short-pubescent above, hirsutulous beneath; peduncles rather stout, 3-7 cm. long, the buds oblong or obconic; flowers in spikes about 8 cm. long, or shorter; calyx subcylindric, densely tomentose, 14-16 mm. long, its ovate-lanceolate teeth acute: corolla densely long-strigose, about 23 mm. long; stamens about 5 cm. long, united below the middle.

Between Pamplonita and Chinácota, Norte de Santander, Colombia, 1300-1800 m. altitude, edge of woods, March 17, 1927, *Killip & Smith 20770*, type (N.Y.). Vicinity of Suratá, Santander, *Killip & Smith 16483*. Vicinity of Medellín, *Archer 59, 558, 8¼1*.

47. **Inga Holtonii** Pittier, Contr. U. S. Nat. Herb. 18: 213. 1916.

Type locality: Cauca River, Colombia.
La Palla, El Valle, *Holton 1004* (type). Buga, El Valle, *Lehmann 779*. El Valle, *Pennell, Killip & Hazen 8152; Killip & Hazen 11043; Killip 11265*. Popayán, *Lehmann 5752*. GUAMO MACHETO, GUAMO BEJUCO.

48. **Inga codonantha** Pittier, Contr. U. S. Nat. Herb. 18: 202, *pl. 102*. 1916.

Type locality: Campoalegre, Colombia.
Colombia, *Mutis 3522, 4919*. Campoalegre, *Langlassé 27* (type). La Mesa, Cundinamarca, *Triana*.

49. **Inga venosa** Griseb. Fl. Brit. W. Ind. 711, hyponym 1864. Benth. Trans. Linn. Soc. 30: 623. 1875.

Type locality: Trinidad.
Medellín, *Toro 843*. Trinidad. Venezuela (?).

50. **Inga fastuosa** Willd. Sp. Pl. 1014. 1806.

Mimosa fastuosa Jacq. Fragm. 15, *pl. 10*. 1809.

Type locality: Caracas, Venezuela
Sonsón, Antioquia, *Archer 656*. Venezuela. GUAMO CAJETO.

51. **Inga villosissima** Benth. Trans. Linn. Soc. 30: 624. 1875.

Type locality; Near Tovar, Venezuela.
Colombia, *Mutis 3648*. Venezuela.

52. **Inga sierræ** Britton & Killip, sp. nov.

Frutex vel arbor parva, ramulis foliorum rachidibus pedunculisque brunneo-tomentosis; rachis anguste alata, glandulis crassis, brevistipitatis; foliola 3–4-juga, coriacea, ovata vel elliptica, acuta vel breviter acuminata, supra laxe pubescentia, demum glabrata, subtus in veniis villosa; flores brevispicati (vel subcapitati?); legumen compressum, curvatum, dense brunneo-tomentosum.

A shrub or small tree, 1.5–5 m. high, with stout twigs, the leaf-rachis and the short stout peduncles densely brown-tomentose. Petiole and rachis 4–10 cm. long, the rachis narrowly winged, the glands stout, short-stipitate; leaflets 3 or 4 pairs, coriaceous, ovate or elliptic, 4–9 cm. long, acute or short-acuminate at apex, obtuse or rounded at base, loosely pubescent, becoming glabrous and lustrous, with impressed veins above, villous, at least on the elevated veins l eneath; fruiting peduncles 2–4 cm. long; flowers short-spicate (or subcapitate?); old calyx long-pubescent, about 10 mm. long, its teeth lanceolate, acute; legume compressed, about 15 cm. long, 2.5–3 cm. wide, about 7 mm. thick, curved, sometimes nearly into a circle, densely brown-tomentose, its margins scarcely elevated.

La Sierra, north of Medellín, Antioquia, Colombia, about 2000 m. altitude, January, 1931, *W. A. Archer 1366*, type (U.S.).

53. **Inga pseudofastuosa** Britton & Killip, sp. nov.

Dense brevipubescens; folii rachis conspicue alata; foliola 3–4-juga, chartacea, late elliptica vel elliptico-obovata, nitida, acuta, subtus crasse reticulata; flores dense spicati; calycis dentes ovati, acuti; corolla dense et longe strigosa, lobis lanceolatis, acutis.

Leaf-rachis stout, densely short-pubescent, conspicuously winged between the pairs of leaflets, the pubescent, strongly veined wings 1–1.5 cm. wide. Leaflets 3 or 4 pairs, chartaceous, broadly elliptic or elliptic-obovate, 10–18 cm. long, 6–11 cm. wide, lustrous, short-pubescent, and faintly veined above, strongly veined, pilose-pubescent, and coarsely reticulate beneath, the apex acute, the base obliquely rounded, the midvein prominent on both sides; peduncles slender, densely short-pubescent, about 10 cm. long; flowers in dense spikes 2–4 cm.

long; calyx about 12 mm. long, densely short-pubescent, its ovate teeth acute; corolla about 2 cm. long, densely long-strigose, its lobes lanceolate, acute; stamens 3–4 cm. long.

Isla brava, Río Magdalena, Colombia, August 6, 1875, *André 216 in part*, type (N.Y.). ?Colombia, *Mutis 3629*. Placed in this relationship with hesitation, the rachis-glands being obscure in the specimens examined.

Inga Fendleriana Benth. (recorded by Bentham with the type locality, Valley of Macarao, in Colombia) was really from Venezuela.

2. ENTEROLOBIUM Mart. Flora 20: Beibl. 117. 1837.

Type species: *Mimosa contortisiliqua* Vell.

1. Enterolobium cyclocarpum (Jacq.) Griseb. Fl. Brit. W. Ind. 226. 1860.

Mimosa cyclocarpa Jacq. Fragm. 30. 1801.
?*Prosopis dubia* H. B. K. Nov. Gen. & Sp. 6: 309. 1824.

Type locality: Caracas, Venezuela.
Santa Marta, *H. H. Smith 932*. Matojiro, *Espina & Giacometto B. 5*. Lands of Loba, Bolívar, *Curran 296*. Bucaramanga, Santander, *Killip & Smith 19064* (cultivated). Venezuela; Panama to Tamaulipas and Sinaloa; Jamaica; Cuba. Widely planted in tropical regions for shade. OREJERO. ANJERA, CARITO, ORIDRA, PIÑÓN.

3. PITHECELLOBIUM Mart. Hort. Monac. 188. 1829.

Type species: *Mimosa Unguis-cati* L.

KEY TO SPECIES OF PITHECELLOBIUM

Flowers spicate.
  Spikes 4–12 cm. long.
    Corolla about 12 mm. long; stamens 5–6
      cm. long .... 1. *P. hymenæœfolium.*
    Corolla 5–7 mm. long; stamens much shorter.
      Ovary glabrous .... 2. *P. spinulosum.*
      Ovary pubescent .... 3. *P. lanceolatum.*
  Spikes only about 1 cm. long, or shorter........ 4. *P. Pittieri.*
Flowers capitate.
  Corolla 2–3 mm. long; stamens white.
    Leaflets glabrous; pods at length glabrate.. 5. *P. dulce.*
    Leaflets pubescent on both sides; pods densely
      pubescent .... 6. *P. microchlamys.*
  Corolla 5–7 mm. long; stamens pink.
    Leaflets obovate, usually emarginate, up to
      2 cm. long .... 7. *P. subglobosum.*
    Leaflets oblong-elliptic, obtusely acuminate,
      longer.
      Flowers and leaflets glabrous.......... 8. *P. forfex.*
      Flowers canescent; leaflets pilosulous 9. *P. pubescens.*

The generic name is often spelled *Pithecolobium* and *Pithecollobium*.

1. Pithecellobium hymenææfolium (H. & B.) Benth. Lond. Journ. Bot. 3: 198. 1844.

Inga hymenæœfolia H. & B.; Willd. Sp. Pl. 4: 1008. 1806.
Pithecellobium panamense Duch. & Walp. Linnæa 23: 746. 1850.

Type locality: Caripe, Venezuela.
Santa Marta, *H. H. Smith 105*. Lands of Loba, Bolívar, *Curran 225*. Goajira, *Dawe 590*. Usiacurí, Atlántico, *Dugand 888*. Panama; Venezuela. PAYANDÍ, UÑA DE TIGRE.

2. **Pithecellobium spinulosum** Pittier, Contr. U. S. Nat. Herb. 20: 459.   1922.

Type locality: Loba, Bolívar, Colombia.
Loba, Bolívar, *Curran 48, 169* (type).   Río Magdalena, Atlántico, *Dugand 520.*   Endemic.   BUCHE, BUCHE BLANCO.

3. **Pithecellobium lanceolatum** (H. & B.) Benth. Lond. Journ. Bot. 5: 105. 1846.

Mimosa ligustrina Jacq. Fragm. 29.   1801.
Inga lanceolata H. & B.; Willd. Sp. Pl. 4: 1005.   1806.
Pithecellobium ligustrinum Klotzsch; Benth. Trans. Linn. Soc. 30: 571. 1875.
Not Benth.   1844.

Type locality: Nova Barcelona (Venezuela).
Common in northern Colombia.   Venezuela; Costa Rica to Sinaloa.   ESPINO, TIRACO, PAYANDÉ, BUCHE, GALLINDRO.

4. **Pithecellobium Pittieri** Britton & Killip.

Pithecellobium oblongum Benth. sensu Pittier, Contr. U. S. Nat. Herb. 20: 463.   1922.   Not Benth.   1844.

Santa Marta, *H. H. Smith 28a*, type (Gray Herb.).   Turbaco, Bolívar, *Killip & Smith 14312.*   Venezuela; Trinidad.

5. **Pithecellobium dulce** (Roxb.) Benth. Lond. Journ. Bot. 3: 199.   1844.

Mimosa dulcis Roxb. Pl. Corom. 1: 67.   1795.

Type locality: Coromandel, East Indies.
Frequent in northern Colombia.   Often confused with *P. Unguis-cati* (L.) Mart., which has glabrous flowers, and is not known to occur in Colombia.   Venezuela; British Guiana; Panama to Sonora.   Much planted for ornament and shade in tropical regions. Naturalized in tropical Asia.   DINDU, OJITO DE NUNA, AZABUCHE, GALLINBRO.

6. **Pithecellobium microchlamys** Pittier, Arb. & Arb. Venez. dec. 4-5: 48.   1925.

Type locality: Barquisimeto, Lara, Venezuela.
Ponedera, Atlántico, *Dugand 777.*   Tocaima, Cundinamarca, *Pérez 2156, 2235.* Guataquí, Cundinamarca, *Pérez.*   TIRACO.

7. **Pithecellobium subglobosum** Pittier, Contr. U. S. Nat. Herb. 20: 463.   1922.

Type locality: Santa Marta, Colombia.
Santa Marta, *H. H. Smith 309, 309a* (co-type).   ?Huila, *Rusby & Pennell 345* (legumes only).   Río Magdalena, *André 1857.*   Endemic.

8. **Pithecellobium forfex** (Kunth) Benth. Lond. Journ. Bot. 3: 199.   1844.

Inga forfex Kunth, Mim. 52, *pl. 16.*   1820.

Type locality: Cartagena, Colombia.
Santa Marta, *H. H. Smith 26, 308;* Barranquilla, *Elias 844, 1109; Dugand 730.* Turbaco, Bolívar, *Killip & Smith 14206, 14338.*   Endemic.   BUCHE COLORADO, TIRACO.

9. **Pithecellobium pubescens** (Bert.) Benth. Journ. Bot. Hook. 2: 141.   1840.

Inga pubescens Bert.; DC. Prodr. 2: 437.   1825.
Inga paniculata Spreng.; DC. Prodr. 2: 437.   1825.

Type locality: Santa Marta, Colombia.
Santa Marta, *H. H. Smith 307, 695, 698.*   Barranquilla, *Elias 335; Paul 43, B. 41.* Cartagena, *Heriberto 278.*   Sincé, Bolívar, *Pennell 4020.*   British Guiana (according to Bentham).

Pithecellobium polycephalum Benth. and *P. multiflorum* (H.B.K.) Benth. recorded from Colombia by Bentham, are not now represented by Colombian specimens in the Kew Herbarium.   They are species with very small flowers and flat legumes, probably related to *Albizzia.*

4. KLUGIODENDRON Britton & Killip, gen. nov.

Arbores inermes; folia bipinnata, pinnis 1-jugis, foliolis 1-jugis, glandula petiolulorum oblonga, sessile; inflorescentia axillaris vel terminalis, floribus

in capitulis globosis, pedunculatis; bracteolæ amplæ; calyx 5-lobatus; corolla 4–5-lobata; stamina ca. 20, infra medium conjuncta; legumen coriaceum, planum, obliquissimum, ad marginem alterum valde crenatum, ad alterum breviter crenatum, curvatum, valvis post dehiscentiam tortuosis; semina arillata, arillo carnoso.

Unarmed trees, the bipinnate leaves with 1 pair of pinnæ, the large leaflets also 1 pair, the petiolules bearing an oblong sessile gland. Inflorescence axillary or terminal, the flowers several or many in peduncled globose heads; bractlets large, as long as the calyx, or longer, deciduous, lanceolate, acuminate. Calyx 5-lobed. Corolla 4–5-lobed. Stamens about 20, united somewhat above the base. Young legume coriaceous, flat, very oblique, deeply crenate on one margin, shallowly crenate on the other, curved, glabrous, very densely transversely veined, the veins anastomosing (*Klug 955*, Loreto, Peru). Mature legume-valves twisting after dehiscence; seeds with a short, white, fleshy aril (according to Poeppig and Endlicher).

Type species: Klugiodendron lætum (Poepp. & Endl.) Britton & Killip (*Inga luta* Poepp.); *Pithecellobium lætum* Benth.; *P. polycarpum* Poepp. & Endl.), a native of Peru.

1. Klugiodendron umbrianum Britton & Killip, sp. nov.

Arbor, ramulis brevipilosis; foliola ovato-lanceolata, longe acuminata, sessilia, supra glabra, subtus in costa laxe strigosa; inflorescentia axillaris, pedunculis brevipilosis; bracteolæ lanceolatæ; calycis dentes piloso-ciliati; corollæ lobi acuti, ciliolati.

A tree, about 6 m. high, the slender twigs loosely short-pilose. Leaves bipinnate, the slender petiole 3.5–5 cm. long; pinnæ 1 pair; petiolules rather stout, 10–13 mm. long, bearing an oblong sessile gland below the leaflets; leaflets 1 pair, sessile, ovate-lanceolate, long-acuminate, submembranous, dull, pinnately and reticulate-veined, 8–11 cm. long, 2.5–4 cm. wide, glabrous above, loosely strigose on the midvein beneath, slightly inequilateral, the base narrowed; inflorescence axillary, of 2 small slender-peduncled heads borne on a rather stout, short-pilose stalk about 2.5 cm. long; peduncles short-pilose, 3.5–4 cm. long; heads few-several-flowered; bractlets lanceolate, acuminate, pilose, 2–3 mm. long; calyx 2 mm. long, its 5 lanceolate teeth pilose-ciliate; corolla about 4 mm. long, its 4 or 5 ovate, acute lobes ciliolate; stamens white, about 6 mm. long, the filaments united to about the middle.

Comisario del Putumayo, Umbría, Colombia, in forest at 325 m. altitude, December, 1930, *G. Klug 1865*, type (N.Y.).

5. ABAREMA Pittier, Arb. & Arb. Legum. 56. 1927; Trab. Mus. Com. Venez. 2: 86. 1927.

[JUPUNBA Britton & Rose, N. Am. Flora 23: 24. 1928]

Type species: *Pithecellobium Avaucmotemo* Mart.

1. Abarema Jupunba (Willd.) Britton & Killip.

Acacia Jupunba Willd. Sp. Pl. 4: 1067. 1806.
Mimosa trapezifolia Vahl, Eclog. 3: 36. 1807.
Pithecellobium trapezifolium Benth. Journ. Bot. Hook. 2: 142. 1840.
Pithecellobium Jupunba Urban, Symb. Ant. 2: 257. 1900.
Abarema trapezifolia Pittier, Arb. & Arb. Legum. 56. 1927; Trab. Mus. Com. Venez. 2: 86. 1927.
Jupunba Jupunba Britton & Rose, N. Am. Flora 23: 27. 1928.
Jupunba trapezifolia Moldenke, Bull. Torrey Club 59: 155. 1932.

Type locality: Pará, Brazil.
Puerto Wilches, Santander, *Killip & Smith 14851*. El Humbo, Boyacá, *Lawrance 161*. French Guiana to Brazil, Bolivia, Trinidad, Tobago and Venezuela; Grenada to Guadeloupe.

6. **PUNJUBA** Britton & Rose, N. Am. Flora 23: 28. 1928.

Type species: *Pithecellobium racemiflorum* Donn. Smith.

KEY TO SPECIES OF PUNJUBA

Leaves glabrous; upper leaflets 12-15 cm. long..   1. *P. Killipii.*
Leaflets pubescent on both sides, 5-8 cm. long....   2. *P. Lehmannii.*

1. **Punjuba Killipii** Britton & Rose, sp. nov.

Arbor, ramulis dense puberulis; foliola 3–4-juga, acuminata, reticulata, glabra, jugo supremo late oblanceolato, ceteris ellipticis vel ovatis; flores in spicis axillaribus pedunculatis puberulis; calycis dentes breves et lati; corollæ lobi ovati, acuti; stamina ultra medium conjuncta; legumen juvenile spirale, latere altero reticulato, altero plano.

A tree, the young twigs densely puberulent, the leaves glabrous, except the short puberulent petiolules. Pinnæ 1 pair; petiole rather stout, 4 or 5 cm. long; rachis slender, bearing a small suborbicular depressed gland between each pair of leaflets; leaflets 3 or 4 pairs, subchartaceous, acuminate, reticulate-veined, the upper pair broadly oblanceolate, about 15 cm. long, the others elliptic to ovate, 7–12 cm. long; flowers white, in dense axillary peduncled puberulent spikes about 10 cm. long, the peduncles 5–12 cm. long; calyx 2 mm. long, its teeth short and broad; corolla 6–7 mm. long, its ovate lobes acute; stamens 10-11 mm. long, united to above the middle; young legume flat, spirally coiled, strongly reticulate-veined on one side, smooth on the other, 7-12 cm. long, about 12 mm. wide, its narrow margins slightly elevated.

Open hills, Salento, Caldas, Colombia 1700-1900 m. altitude, July 25-31, 1922 *Killip 9048*, type (N Y.). A barren specimen from Cali (*André ?625*), with glabrous, similar leaflets, may be referable to this species.

2. **Punjuba Lehmannii** Britton & Rose, sp. nov.

Dense puberula; foliola 3–4-juga, ovata, elliptica vel (suprema) obovato-elliptica, supra brevipubescentia, subtus pilosa, rachidis glandulis depressis; spicæ axillares; calycis dentes acuti; corollæ lobi ovato-oblongi, acuti; stamina alte in tubum connata.

Twigs, petioles, leaf-rachises and inflorescence densely puberulent. Petioles rather stout, 1.5–4 cm. long; rachis bearing an inconspicuous depressed gland between some of the pairs of leaflets; pinnæ 1-pair; leaflets 3 or 4 pairs, subchartaceous, acute, ovate, elliptic, or (the upper ones) obovate-elliptic, 5–8 cm. long, reticulate-veined, dark green and loosely short-pubescent above, pale and rather densely pilose beneath; spikes axillary, dense, about 12 cm. long, on peduncles 3–4 cm. long; calyx 2.5 mm. long, its ovate teeth acute; corolla about 6 mm. long, with ovate-oblong acute lobes; stamens about 12 mm. long, united to much above the middle; legume spirally coiled, about 20 cm. long 1–1.2 cm. wide, glabrous, the margins slightly elevated.

Nopaya, Colombia, 1600-2000 m. altitude, *Lehmann B.T. 364*, type (N Y, fruiting specimen at Kew), *8623*.

7. **COJOBA** Britton & Rose, N. Am. Flora 23: 29. 1928.

Type species: *Mimosa arborea* L.

KEY TO SPECIES OF COJOBA

Leaves bipinnate; leaflets 15–30 pairs, 6–8 mm. long..   1. *C. colombiana.*
Leaves once pinnate; leaflets few pairs, 2–12 cm. long.
   Leaflets 4–8 pairs, 2–6 cm. long................   2. *C. tubulifera.*
   Leaflets 1–5 pairs, 3–12 cm. long................   3. *C. rufescens.*

1. **Cojoba colombiana** Britton & Killip, sp. nov.

Rami juveniles foliorum rachis pedunculique dense puberula; folia bipinnata, glandulis sessilibus, rotundis, pinnis 13–17-jugis, fere sessilibus,

foliolis 18–30 jugis, anguste oblongo-lanceolatis, obtusis, glabris, costa excentrica; pedunculi solitarii vel bini; capitula globosa, multiflora; calyx campanulatus; corolla subtubulosa; legumen stipitatum, inter semina alte constrictum, glabrum.

Young branches, laef-rachis and peduncles densely puberulent. Leaves bipinnate, 1.5–2 cm. long; petioles 2–3 cm. long; rachis bearing sessile circular glands 0.5–0.8 mm. in diameter between many of the pairs of pinnæ; pinnæ 13–17 pairs, very nearly sessile, 5–8 cm. long; leaflets 18–30 pairs, narrowly oblong-lanceolate, slightly curved upward, subchartaceous, glabrous, obtuse, faintly veined with the midvein excentric, 6–8 mm. long, about 2 mm. wide; peduncles solitary, or 2 together in the axils, very slender, 2–3 cm. long; heads globose, about 1.5 cm. in diameter, many-flowered; calyx campanulate, 2 mm. long, 5-toothed; corolla nearly tubular, 5 mm. long, 5-toothed, the ovate teeth acute; stamens about 10 mm. long, united below the middle; legume about 8 cm. long, or longer, stipitate, very deeply constricted between the seeds, the seed-bearing portions ellipsoid, 8–12 mm. long, nearly 10 mm. in diameter, glabrous, reticulate-veined.

Vicinity of Medellín, Antioquia, Colombia, 1927, *R. A. Toro 241*, type (N.Y.).

2. Cojoba tubulifera (Benth.) Britton & Rose, N. Am. Flora 23: 32. 1928.

Inga tubulifera Benth. Lond. Journ. Bot. 4: 584. 1845.
Pithecellobium tubuliferum Pittier, Contr. U. S. Nat. Herb. 18: 181. 1916.

Type locality: Panama.
Northwestern Colombia, *Barclay*. Panama.

3. Cojoba rufescens (Benth.) Britton & Rose, N. Am. Flora 23: 32. 1928.

Inga rufescens Benth. Lond. Journ. Bot. 4: 585. 1845.
Inga globulifera Benth. loc. cit. 1845.
Inga Billbergiana Benth. loc. cit. 1845.
Pithecellobium rufescens Pittier, Contr. U. S. Nat. Herb. 18: 181. 1916.

Type locality: Island off the coast of Veraguas, Panama.
La Mojana, Atlántico, *Dugand 604*. Panama.

8. ARTHROSAMANEA Britton & Rose, gen. nov.

Arbores fruticesve inermes; folia bipinnata; inflorescentia racemosa, racemis axillaribus vel terminalibus, floribus in fasciculis brevipedunculatis; calyx 5-dentatus; corolla 5-lobata; stamina numerosa, parte connata; legumen planum vel compressum, lineare, inter semina septatum, demum in articulos secedens, marginibus undulatis.

Unarmed trees or shrubs with bipinnate leaves. Inflorescence racemose, the racemes axillary or terminal, the flowers sessile, in dense short-peduncled clusters. Calyx 5-toothed. Corolla 5-lobed. Stamens numerous, their filaments partly united. Legume flat or compressed, linear, narrow, septate between the seeds, ultimately breaking transversely, its margins undulate.

Type species: *Mimosa pistaciæfolia* Willd.

1. Arthrosamanea pistaciæfolia (Willd.) Britton & Rose.

Mimosa pistaciæfolia Willd. Sp. Pl. 4: 1028. 1806.
Samanea pistasiæfolia Dugand, Apunt. Hist. Nat. Dept. Atlántico 31. 1933.
Pithecellobium pistaciæfolium Standl.; Dugand, Apunt. Hist. Dept.
    Atlántico 31. 1933, as synonym.

Type locality: Caracas, Venezuela.
San Martín de Loba, Bolívar, *Curran 43, 44*. Estrella, Bolívar, *Curran 300*. Ponedera, Atlántico, *Dugand 309*. Gamarra, Magdalena, *Dawe 467*. Venezuela, and perhaps Ecuador. GUAYACÁN CHAPARRO, GUAYACÁN HOBO, GUAYACÁN CDNEGA.

9. **SAMANEA** Merrill, Journ. Wash. Acad. Sci. 6: 46. 1916.

Type species: *Mimosa Saman* Jacq.

1. **Samanea Saman** (Jacq.) Merrill, Journ. Wash. Acad. Sci. 6: 47. 1916.

Mimosa Saman Jacq. Fragm. 15. 1800.
Inga salutaris H. B. K. Nov. Gen. & Sp. 6: 304. 1823.
Pithecellobium Saman Benth. Lond. Journ. Bot. 3: 216. 1844.

Type locality: Caracas, Venezuela.
Frequent in Colombia, much planted for shade, as throughout tropical America. Venezuela; Panama to Nicaragua. SAMÁN, CAMPANO.

10. **CHLOROLEUCON** (Benth.) Britton & Rose, N. Am. Flora 23: 36. 1928.

[CATHORMIUM Hassk. sens. Pittier, Arb. & Arb. Legum. 54. 1927. Trab. Mus. Com. Venez. 2: 84. 1927, not Hassk.]

Type species: *Pithecellobium vincentis* Benth.

KEY TO SPECIES OF CHLOROLEUCON

Leaflets 8–10 pairs, linear, 4–7 mm. long.............. 1. *C. mangense.*
Leaflets 3–6 pairs, elliptic to obovate, 6–9 mm. long... 2. *C. bogotense.*

1. **Chloroleucon mangense** (Jacq.) Britton & Rose, N. Am. Flora 23: 38. 1928.

Mimosa mangensis Jacq. Enum. 34. 1760.
Mimosa parvifolia Sw. Fl. Ind. Occ. 984. 1800.
Inge marthæ Spreng.; DC. Prodr. 2: 441. 1825.
Pithecellobium parvifolium Benth. Lond. Journ. Bot. 3: 223. 1844.
Pithecellobium mangense Macbr. Contr. Gray Herb. 59: 3. 1919.
Enterolobium mangense Fawcett & Rendle, Fl. Jam. 4: 151. 1920.
Cathormium mangensis Dugand, Apunt. Hist. Nat. Dept. Atlántico 32. 1933.

Type locality: Mango Island, Cartagena, Colombia.
Santa Marta, *H. H. Smith 2064, 2065.* Barranquilla, *Elias 186.* Arjona, Bolívar, *Killip & Smith 14494.* Panama; Jamaica; French Guiana (according to Bentham); Brazil. OLLA DE ZORRO.

2. **Chloroleucon bogotense** Britton & Killip, sp. nov.

Ramuli inermes; petioli brevipilosi, glandula conica vel subcylindrica; pinnæ 2–3-jugæ; foliola 3–6-juga, elliptica vel elliptico-obovata, glabra, obtusa vel rotundata, costa subexcentrica; pedunculi solitarii vel bini vel terni; flores glabri; stamina infra medium conjuncta.

Twigs very slender, unarmed, glabrous. Petioles and leaf-rachises slender, short-pilose, 2–4 cm. long; petiolar gland conic to subcylindric, about 0.4 mm. in diameter; pinnæ 2 or 3 pairs; rachillæ short-pilose, 1–3 cm. long; leaflets 3–6 pairs, elliptic or elliptic-obovate, membranous, at least when young, glabrous, obtuse or rounded, 6–9 mm. long, obscurely veined above, several-nerved and pinnately veined beneath, the midvein slightly excentric; peduncles solitary, or 2 or 3 together, glabrous, 10–16 mm. long; flowers capitate, glabrous; heads several-flowered; calyx about 2 mm. long; corolla about 4 mm. long; stamens about 8 mm. long, united below the middle.

Anapoima, near Bogotá, Cundinamarca, Colombia, 500 m. altitude, *Triana 4481,* type (N.Y.). Without locality, *Mutis 4911.* ANGARILLO.

11. **ZYGIA** P. Browne; St. Hil. Expos. Fam. Nat. 2: 246. 1805.

Type species: *Mimosa latifolia* L.

KEY TO SPECIES OF ZYGIA

Flowers capitate.
 Twigs and leaves glabrous or very nearly so;
  legume 10–15 mm. wide................... 1. *Z. latifolia.*

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Twigs and leaf-rachises pubescent; legume about
2 cm. wide .... 2. *Z. pilosula.*
Flowers spicate or racemose.
Petiole very short, or pinnæ sessile; leaflets
1–2 pairs .... 3. *Z. longifolia.*
Petiole 2–3 cm. long; leaflets 4–6 pairs, very large 4. *Z. Lehmannii.*

1. Zygia latifolia (L.) Fawcett & Rendle, Fl. Jam. 4²: 150. 1920.

Mimosa latifolia L. Syst. ed. 10, 1310. 1759.
Pithecellobium latifolium Benth. Lond. Journ. Bot. 3: 214. 1844.

Type locality: Jamaica.
Santa Marta, *H. H Smith 929; Seifriz 371.* Villavicencio, Meta, *Pennell 1574;* Puerto Wilches, Santander, *Killip & Smith 21131.* Jamaica: Martinique; St. Vincent; Surinam (according to Bentham); Trinidad; Venezuela; Bolivia; Brazil.

2. Zygia pilosula (Pittier) Britton & Rose.

Pithecellobium pilosulum Pittier, Contr. U. S. Nat. Herb. 20: 466. 1922.

Type locality: San Martín de Loba, Bolívar, Colombia.
Bolívar, *Curran 19, 88* (type). Without locality, *Mutis 3535, 3645, 4971.* ?Venezuela. GUAMO MACHO.

3. Zygia longifolia (H. & B.) Britton & Rose, N. Am. Flora 23: 40. 1928.

Inga longifolia H. & B.; Willd. Sp. Pl. 4: 1010. 1806.
Pithecellobium ligustrinum Benth. Lond. Journ. Bot. 3: 213. 1844.
Pithecellobium Vahlianum Benth. Trans. Linn. Soc. 30: 594. 1875.

Type locality: Tropical America.
Frequent in Colombia. Panama to Nicaragua. AuÑ.

4. Zygia Lehmannii (Harms) Britton & Rose.

Pithecellobium Lehmannii Harms, Repert. Sp. Nov. Fedde 17: 92. 1921.

Type locality: Río Cofre, Popayán, Colombia
Known to us only from description of the type specimen *(Lehmann 8989).*
Endemic.

12. HAVARDIA Small, Bull. N. Y. Bot. Gard. 2: 91. 1901.

Type species: *Pithecellobium brevifolium Benth.*

1. Havardia platyloba (Spreng.) Britton & Rose, N. Am. Flora 23: 43. 1928.

Acacia platyloba Spreng. Syst. 3: 144. 1826.
Pithecellobium sericiflorum Benth. Lond. Journ. Bot. 5: 105. 1846.
Pithecellobium platylobum Urban, Symb. Ant. 5: 360. 1908.

Type locality: Magdalena River, Colombia.
Santa Marta, *H. H. Smith 30, 52; Record 51; Killip & Smith 11090,* legumes only. Venezuela; Aruba; Yucatán.

13. PSEUDOSAMANEA Harms, Notizbl. 11: 54. 1930.

Type species: *Acacia Guachapele* H. B. K.

1. Pseudosamanea Guachapele (H. B. K.) Harms, Notizbl. 11: 54. 1930.

Acacia Guachapele H. B. K. Nov. Gen. &. Sp. 6: 281. 1824.
Lysiloma Guachapele Benth. Trans. Linn. Soc. 30: 533. 1875.
Pithecellobium longepedatum Pittier, Contr. U. S. Nat. Herb. 20: 464. 1922.
Samanea samaniqua Pittier, Arb. & Arb. Venez. dec. 4–5: 54. 1925.
Albizzia longepedata Britton & Rose; Record, Tropical Woods 11: 14. 1927.

Type locality: Near Guayaquil, Ecuador.
Santa Marta, *Rusby & Pennell 253, 322.* Barranquilla, *Elias 123, 509.* Medellín, *Daniel 37.* Tocaima, Cundinamarca, *Pérez 2230.* Nariño, Cundinamarca, *Pérez 462.* Costa Rica to Ecuador and Venezuela. TABACA, GUAMARILIO.

14. **MACROSAMANEA** Britton & Rose, gen. nov.

Arbores inermes; folia bipinnata, glandulifera; flores magni, in capitulis pedunculatis; calyx anguste campanulatus, elongatus, 5-dentatus; corolla elongata, 5-lobata; stamina numerosa, parte connata; legumen subplanum, chartaceum, per unum marginem dehiscens.

Unarmed trees, with bipinnate glanduliferous leaves, the very large flowers in peduncled heads. Calyx narrowly campanulate, elongated, 5-toothed. Corolla elongated, 5-lobed. Stamens numerous, long, their filaments partly united. Legume nearly flat, glabrous, chartaceous, longitudinally dehiscent along one suture.

Type species : *Inga adiantifolia* Kunth.

1. **Macrosamanea discolor** (H. & B.) Britton & Rose.

Inga discolor H. & B.; Willd. Sp. Pl. 4: 1023. 1806.
Mimosa discolor Poir. in Lam. Encycl. Suppl. 1: 46. 1810.
Inga adiantifolia Kunth, Mim. 66, *pl. 21.* 1820.
Pithecellobium adiantifolium Benth. Lond. Journ. Bot. 3: 218. 1844.
Samanea adiantifolia Pittier, Arb. & Arb. Venez. dec. 4-5: 55. 1925.

Type locality : Atabapo River (Venezuela-Colombia Boundary).

Known to us from Colombia only from the descriptions and Kunth's illustration. The tree here referred by authors, from British Guiana, appears to be a distinct species.

15. **ALBIZZIA** Durazz. Mag. Tosc. 3: 11. 1772.

Type species : *Albizzia Julibrissin* Durazz.

KEY TO SPECIES OF ALBIZZIA

Leaflets oblong to obovate, 2–4 cm. long; legume 12–20
   cm. long, glabrous; heads large................   1. *A. Lebb. ck.*
Leaflets linear to oblong, much smaller; heads small.
   Legume densely pubescent; leaflets pubescent...   2. *A. carbonaria.*
   Legume (as far as known) glabrous.
      Heads borne in terminal and axillary panicles.
         Glabrous throughout ....   3. *A. colombiana.*
         Leaves pubescent; flower-buds canescent.   4. *A. longipes.*
      Heads solitary, axillary, long-peduncled.
         Flowers densely appressed-pubescent;
           leaflets elliptic ....   5. *A. dubia.*
         Flowers glabrous; leaflets linear-oblong.   6. *A. martha.*

1. **Albizzia Lebbeck** (L.) Benth. Lond. Journ. Bot. 3: 87. 1844.

Mimosa Lebbeck L. Sp. Pl. 516. 1753.

Type locality : Upper Egypt.
Vicinity of Medellín, *Toro 483.* Widely planted and naturalized in tropical America. Native of the Old World tropics.

2. **Albizzia carbonaria** Britton; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 6: 348. 1926.

Albizzia malacocarpa Standley; Britton & Rose, N. Am. Flora 23: 44. 1928.

Type locality : Grown at the Forest Station, Río Piedras, Porto Rico, from seed from Palmira, Colombia.
Frequent at middle elevations in Colombia. Panama ; El Salvador. MUCHE BLANCO, PISQUIN, CARBONERO DE SOMBRIO, GUAMUCHE, DORMILÓN, BAYETO ANTIOQUEÑO, PIÑÓN.

3. **Albizzia colombiana** Britton, sp. nov.

Arbor glaberrima ; pinnæ 2–5-jugæ, petiolis ad vel infra medium glanduliferis, foliolis 15–25-jugis, anguste oblongo-lanceolatis, chartaceis, obtusis;

paniculæ parvæ, axillares et terminales; calycis dentes subacuti; corollæ lobi lanceolati, acuti; stamina pluria, ultra medium conjuncta; legumen chartaceum, glabrum.

A tree, about 15 m. high, or lower, glabrous throughout, the twigs slender. Petioles 2–5 cm. long, bearing a sessile, orbicular, slightly elevated gland near or below the middle; leaf-rachis 6–10 cm. long; pinnæ 2–5 pairs, the rachillæ 6–9 cm. long; leaflets 15–25 pairs, narrowly oblong-lanceolate, chartaceous, obtuse, 4-nerved at base, sparingly and irregularly pinnate-veined, 10–14 mm. long, about 2 mm. wide; heads forming small axillary and terminal panicles about 8 cm. long, or shorter; peduncles slender, 2–4 cm. long; calyx 2 mm. long, its short broad teeth acutish; corolla 5 mm. long, its lobes lanceolate, acute; stamens many, 7–10 mm. long, united to above the middle; legume flat, chartaceous, glabrous, about 15 cm. long and 2 cm. wide, the apex obtuse, short-tipped, the base narrowed.

Near Bonda, Santa Marta, Magdalena, Colombia, August 3, 1899, *H. H. Smith 38*, type (N.Y.); *38a; 2067; Record 75*. ?Tierrabomba Island, Bolivar, *Killip & Smith 14131*.

4. Albizzia (?) longipes Britton & Killip, sp. nov.

Arbor grandis; petioli infra medium glanduliferi, glandula oblonga, subconcava; pinnæ 4–6-jugæ, foliolis 20–30-jugis, linearibus, acutis, membranaceis, dense puberulis; capitula globosa, in paniculis parvis; alabastra canescentia; calycis dentes ovati, acuti; corollæ lobi oblongo-lanceolati; stamina 60 et ultra, ad medium conjuncta.

A large tree, the twigs and the very slender petioles glabrous. Petioles 4–6 cm. long, bearing below the middle, a sessile, oblong, slightly concave gland, about 2 mm. long; leaf-rachis only 2 or 3 cm. long, with 4–6 pairs of pinnæ about 2 cm. long, or shorter; leaflets 20–30 pairs, linear, membranous and densely puberulent-canescent when young, approximate, acute, about 3 mm. long and 0.5 mm. wide, the venation obscure; heads small, globose, numerous, in small terminal and axillary panicles; peduncles slender, glabrous, 4 cm. long, or shorter; flower-buds canescent; calyx 2.5 mm. long, its teeth ovate, acute; corolla 5 mm. long, its lobes oblong-lanceolate, obtuse; stamens 60 or more, nearly 10 mm. long, united to about the middle.

Sabana larga, vicinity of Barranquilla, Atlántico, Colombia, February, 1928, *Brother Elias 499*, type (N.Y.). CARO.

5. Albizzia (?) dubia Britton & Killip, sp. nov.

Ramuli foliorum rachis pedunculique brevipilosa; rachidis glandulæ 1–2, orbiculatæ, subplanæ; pinnæ 5–7-jugæ, foliolis 10–16-jugis, oblique ellipticis, subcoriaceis, apice rotundis, basi truncatis, ciliolatis, supra glabris, subtus in costa pilosulis; pedunculi solitarii, filiformes; flores capitati, dense appresso-pubescentes; calycis dentes ovati; corollæ lobi ovato-lanceolati; stamina infra medium conjuncta.

Twigs, leaf-rachis and peduncles short-pilose. Rachis bearing 1 or 2, orbicular, sessile, nearly flat glands about 1 mm. in diameter; petiole short; rachis 5–7 cm. long; pinnæ 5–7 pairs; rachillæ short-pilose, 2.5–5 cm. long; leaflets 10–16 pairs, obliquely elliptic, subcoriaceous, 4–7 mm. long, 2–3 mm. wide, rounded at apex, truncate at base, ciliolate, glabrous above, pilosulous on midnerve beneath, the nearly central midvein elevated beneath, the pinnate lateral venation obscure; peduncles axillary, solitary, filiform, 3–6 cm. long; flowers capitate, densely appressed-pubescent; calyx 1.5 mm. long, its teeth ovate; corolla 4 mm. long, deeply lobed, the lobes ovate-lanceolate, acute; stamens about 12, about 7 mm. long, united below the middle.

Colombia, 1760-1808, *Mutis 3531*, type (U.S.).

6. **Albizzia marthæ** Britton & Killip, sp. nov.

Ramuli glabri; petioli rachisque tenuissima, brevipubescentia; glandula petiolaris orbiculata, subelevata; pinnæ 6–8-jugæ, rachillis filiformibus, foliolis 12–16-jugis, lineari-oblongis, membranaceis, glabris, subacutis; capitula solitaria, pedunculis tenuissimis; flores glabri; calyx anguste campanulatus, subtruncatus; corollæ lobi lanceolati, acuti; stamina ultra medium conjuncta.

Twigs slender, glabrous. Petiole and leaf-rachis very slender, loosely short-pubescent, 5–7 cm. long, the petiole bearing an orbicular, slightly elevated gland about 1 mm. in diameter, or smaller; stipules oblong to elliptic, 3–12 mm. long, longitudinally striate, obtuse; pinnæ 6–8 pairs, 3–5 cm. long, the rachilla filiform; leaflets 12–16 pairs, linear-oblong, membranous, glabrous, acutish, 3–6 mm. long, 1–2 mm. wide, 4-nerved at base, the midnerve slightly excentric, the lateral venation meagre or obscure; heads solitary, several-many-flowered, axillary, on very slender peduncles 1.5–2 cm. long; flowers glabrous; calyx narrowly campanulate, subtruncate, about 3 mm. long; corolla 5-lobed, about 6 mm. long, the lanceolate lobes acute; stamens many, about 12 mm. long, the filaments united to above the middle.

Santa Marta, Magdalena, Colombia, about 80 m. elevation. *H. H. Smith 296*, type (U.S.).

16. CALLIANDRA Benth. Journ. Bot. Hook. 2: 138. 1840.
[ANNESLIA Salisb. Parad. Lond. *pl. 64*. 1807]

Type species: *Calliandra Houstoni* (L'Hér.) Benth.

KEY TO SPECIES OF CALLIANDRA

A. Leaflets only 1 or 2 pairs, large, 2–10 cm. long.
  Leaflets subfalcate, acuminate, 7–15 cm. long.
    Heads large, many-flowered, axillary...... 1. *C. carbonaria*.
    Heads very small, few-flowered, panicled.... 2. *C. microcephala*.
  Leaflets oblong, acute or obtuse, 2–7 cm. long.... 3. *C. glaberrima*.
B. Leaflets several or many, smaller.
  1. Leaflets chartaceous or subcoriaceous.
    a. Pinnæ only 1 or 2 pairs.
      *Leaflets 7–20 mm. long.
        Calyx teeth linear-lanceolate...... 4. *C. angustidens*.
        Calyx teeth ovate (as far as known).
          Leaflets 4 or 5 pairs......... 5. *C. medellinensis*.
          Leaflets 8–15 pairs.
            Leaflets softly pubescent, dull, papillose.......... 6. *C. santanderensis*.
            Leaflets glabrous, lustrous, smooth.
              Leaflets 3–4 mm. wide, acute or subacute.... 7. *C. Schultzei*.
              Leaflets 4–6 mm. wide, rounded .... 8. *C. colombiana*.
      **Leaflets only 6–7 mm. long, obtuse.... 9. *C. magdalenæ*.
    b. Pinnæ several or many pairs.
      Calyx 5–7 mm. long.
        Corolla densely sericeous with long brown hairs: leaflets 20 pairs or fewer, about 1 cm. long.......... 10. *C. tolimensis*.
        Corolla glabrous: leaflets 25 pairs or more, less than 5 mm. long.. 11. *C. Purdiei*.
      Calyx 1.5–3 mm. long.
        Leaflets less than 1.5 mm. wide. 12. *C. Pittieri*.
        Leaflets 2–4 mm. wide.
          Leaflets 12–18 pairs, minutely ciliolate, smooth .... 13. *C. diversifolia*.

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            Leaflets  30–40  pairs,  pubescent,
                scaberulous ................. 14. C. glomerulata.
    2. Leaflets membranous or thin.
        Leaflets several to many pairs, linear to
        oblong, 1–5 mm. wide.
            Leaflets pubescent or ciliate.
                Leaflets linear-oblong, 10–16 mm.
                    long ......................... 15. C. flavida.
                Leaflets linear, 2–4 mm. long...... 16. C. caracasana.
            Leaflets glabrous.
                Stems 4-sided ................... 17. C. tetragona.
                Stems terete .................... 18. C. Toroana.
    Leaflets 3–6 pairs, elliptic to obovate, much
        wider ................................. 19. C. marginata.
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1. Calliandra carbonaria Benth. Lond. Journ. Bot. 3: 95. 1844.

Type locality: Popayán, Colombia
Nopaya, *Lehmann B. T. 565.* Tolima, *Lehmann 4070.* Dept. El Cauca, *Hartweg 964* (type); *Lehmann 2089; André 2755.* Putumayo *Klug 1716.* Ecuador.

2. Calliandra microcephala Britton & Killip, sp. nov.

Glabra; pinnæ 1-jugæ, foliolis sesqui-jugis, oblique cllipticis, membranaceis, longe acuminatis, ad basim rotundatis vel angustatis; inflorescentia paniculata, capitulis parvis in fasciculis remotis, pedunculis filiformibus; calycis dentes acuti; stamina infra medium conjuncta.

Glabrous throughout. Petioles slender, 6–7 cm. long; pinnæ 1 pair, the rachilla 2–2.5 cm. long; leaflets 1½ pairs, very obliquely elliptic, membranous, 6-nerved, reticulate-veined, 6–9 cm. long, 2–3.5 cm. wide, the apex acute or sharply long-acuminate, the base rounded or narrowed; inflorescence a very slender panicle, 18–27 cm. long, the small heads in distant fascicles; peduncles filiform, about 2.5 cm. long, or shorter; calyx 1.2 mm. long, its teeth acute; corolla 3 mm. long, its ovate lobes acute; stamens many, about 4 mm. long, united below the middle.

Colombia, 1760–1808, *Mutis 407,* type (U.S.), *3800.*

Similar to *C. amazonica* Benth., of Peru, which has two pairs of leaflets and shorter panicles.

3. Calliandra glaberrima (Benth.) Britton & Killip.

Calliandra glyphoxylon glaberrima Benth. Trans. Linn. Soc. 30: 539. 1875.

Type locality: Valley of the Magdalena, Colombia.
Río Magdalena, *Dawe 470.* Lands of Loba, Bolívar, *Curran.* Natagaima, Huila, *Rusby & Pennell 249, 1156.* Cundinamarca, *Pérez 511, 582; Holton 999; André 1555.* Medellín, *Toro 109A.* Río Tutunendo, El Chocó, *Archer 2188.* Without locality, *Mutis 442.* CLAVELLINA PICHINDÉ.

4. Calliandra angustidens Britton & Killip, sp. nov.

Ramuli dense puberuli; pinnæ 1-jugæ, rachide dense puberula, foliolis 10-16-jugis, subcoriaceis, lineari-lanceolatis, acutis, glabratis, ciliatis, costa subexcentrica; pedunculi crassi; calycis dentes lineari-lanceolati; corolla glabra, lobis acutis; stamina ca. 25, multo ultra medium conjuncta; legumen lineari-oblanceolatum, glabrum, valde reticulatum.

Woody, the branches long, densely puberulent. Petioles about 10 mm. long, or shorter; pinnæ 1 pair, 4–5 cm. long, the slender rachis densely puberulent; leaflets 10–16 pairs, subcoriaceous, linear-lanceolate, acute, ciliate, otherwise glabrate, 7–11 mm. long, 2 mm. wide, finely reticulate-veined, the midvein slightly excentric; stipules lanceolate, acuminate, several-nerved, about 8 mm. long; peduncles stout, puberulent, 8–10 mm. long, bracteolate under the flowers; heads several-many-flowered; calyx about 4 mm. long, 5-toothed, the

teeth linear-lanceolate; corolla glabrous, 8 mm. long, 4–5-lobed, the ovate lobes acute; stamens about 25, nearly 25 mm. long, their filaments united to much above the middle; legume linear-oblanceolate, glabrous, strongly reticulate-veined, 5–7 cm. long, 6–7 mm. wide, its margins elevated; seeds elliptic, 3–4 mm. long.

Villavicencio, Meta, Colombia, January, *E. Pérez Arbelaez 195,* type (U.S.).

5. Calliandra medellinensis Britton & Rose, sp. nov.

Ramuli et pedunculi laxe pilosi; pinnæ 1-jugæ, foliolis 4–5-jugis, oblique lanceolatis vel (infimis) ovato-lanceolatis, chartaceis, ciliatis, acutis vel subobtusis, ad basim subcordatis vel rotundatis, trinerviis; flores capitati; calycis dentes ciliati; corolla 4-lobata, lobis ovatis, acutis; stamina ca. 6 mm. supra basim conjuncta.

Twigs and peduncles slender and loosely pilose. Stipules triangular-lanceolate, striate, long-acuminate, 4–5 mm. long; petioles 6–10 mm. long, pilose; pinnæ 1 pair, 4–5 cm. long; leaflets 4 or 5 pairs, obliquely lanceolate, or the lower pair ovate-lanceolate, chartaceous, ciliate, otherwise glabrous, 3-nerved, finely reticulate-veined, faintly lustrous above, 1–2 cm. long, 4–6 mm. wide, the apex acute or obtusish, the base subcordate or rounded; peduncles about 3 cm. long; flowers capitate; calyx 2.5 mm. long, 5-toothed, the teeth ciliate; corolla about 6 mm. long, glabrous, 4-lobed, the lobes ovate, acute; stamens about 2.5 cm. long, united for about 6 mm. above the base.

Vicinity of Medellín, Antioquia, Colombia, March 23, 1927, *Toro 109,* type (N.Y.).

6. Calliandra santanderensis Britton & Rose, sp. nov.

Arbor, ramulis petiolis rachillisque dense et breviter pilosis; pinnæ 2-jugæ, foliolis 10–15-jugis, oblique oblongis, obtusis, chartaceis, brevipubescentibus, costa subcentrale; legumen lignosum, 7-spermum, marginibus latis, crassis, striatis.

A tree, 5–6 m. high, twigs, petioles and leaf-rachillas densely short-pilose. Stipules lanceolate, striate, about 6 mm. long; petioles only about 3 mm. long; pinnæ 2-pairs, 8–10 cm. long; leaflets 10–15 pairs, chartaceous, obliquely oblong, obtuse, 4-nerved, strongly reticulate-veined, dull, short-pubescent on both sides, ciliate, 15–20 mm. long, 5–8 mm. wide, or the lowest pair smaller. the costa nearly central; legume woody, densely puberulent, 10 cm. long, 14 mm. wide, elastically dehiscent, 7-seeded, its broad thick margins longitudinally striate; seeds obliquely ellipsoid, compressed, about 8 mm. long, minutely mottled.

Río Suratá Valley, near Bucaramanga, Santander, Colombia, 400–600 m. altitude, thickets, December 28, 1926, *Killip & Smith 16205,* type (N.Y.).

7. Calliandra Schultzei Harms, Repert. Sp. Nov. Fedde 24: 209. 1928.

Type locality: Northern base of the Sierra Nevada, Santa Marta, Colombia.
Río Piedras, Sierra Nevada de Santa Marta, Magdalena, *Schultze 553* (photograph and fragment of type). La Esmeralda, Norte de Santander, *Killip & Smith 20926.* Endemic.

8. Calliandra colombiana Britton & Rose, sp. nov.

Arbor humilis, ramulis petiolis rachillisque brevipilosis; pinnæ 1-jugæ, foliolis 9–16-jugis, oblongis, rotundis vel obtusis, ad basim oblique truncatis, subchartaceis, glabris, supra lucentibus; capitula paucifasciculata vel solitaria; flores glabri; calycis dentes obtusi; corollæ lobi acuti; stamina 10–13, multo infra medium conjuncta; legumen lineare, lignosum, marginibus valde crassis.

A low tree, the slender twigs, the petioles and leaf-rachillas short-pilose. Stipules linear-lanceolate, acuminate, about 5 mm. long; petioles 6–12 mm. long; pinnæ 1 pair, 6–9 cm. long; leaflets 9–16 pairs, oblong, subchartaceous, glabrous, 4-nerved, and finely reticulate-veined, 10–15 mm. long, 4–6 mm.

wide, lustrous above, the apex rounded or obtuse, the base obliquely truncate; heads few-together or solitary, on loosely pubescent peduncles about 12 mm. long, or shorter; flowers glabrous; calyx 2 mm. long, its teeth obtuse; corolla 4 mm. long, its ovate lobes acute; stamens few (10–13), 20–25 mm. long, united much below the middle; legume linear, woody, about 10 cm. long, 13 mm. wide, the apex rounded, the margins of the valves much thickened and longitudinally striate, the narrow median surface glabrous, strongly obliquely veined.

Colombia, Natagaima, Huila, altitude 450–500 m, August 12, 1917, *Pennell 1153*, type (N.Y.). Piedras, Mariquita, Tolima, *Triana 4479*. Icononzo, Tolima, *André 1511 bis*. Without locality, *Mutis 3533*. RAYADO.

9. Calliandra magdalenæ (Bert.) Benth. Lond. Journ. Bot. 5: 102. 1846.

Acacia magdalenæ Bert.; DC. Prodr. 2: 455. 1825.
Anneslia magdalenæ Britton & Rose, N. Am. Flora 23: 60. 1928.

Type locality: Santa Marta, Colombia.
Santa Marta, *H. H. Smith 82*. Venezuela; Ecuador (according to Bentham); Panama.

10. Calliandra tolimensis Taubert, Bot. Jahrb. 21: 314. 1895.

Type locality: Tolima, Colombia.
Known to us only from photograph and fragment of type (*Stuebel 239*).

11. Calliandra Purdiei Benth. Lond. Journ. Bot. 4: 104. 1846.

Calliandra clavellina Karst. Fl. Col. 1: 159, *pl. 79*. 1858-61.

Type locality: Mountains of Ocaña, Colombia.
Santander, *Killip & Smith 14982, 16177*. Medellín, *Toro 25*. Dept. Cundinamarca, *Dawe 47*. Ocaña, *Purdie* (type); *Schlim 203*. Endemic. CARBONERO, applied to many species of this genus, CLAVELLINA.

12. Calliandra Pittieri Standley, Contr. U. S. Nat. Herb. 18: 104. 1916.

(See Plate I)

Calliandra bella Trianæ Benth. Trans. Linn. Soc. 30: 556. 1875.
Calliandra Lehmannii Harms, Repert. Sp. Nov. Fedde 17: 90. 1921.
Anneslia Pittieri Britton & Rose, N. Am. Flora 23: 63. 1928.

Type locality: La Esmeralda, Colombia.
El Valle: *Pittier 951* (type); *Lehmann 5367* (type of *C. Lehmannii*); *Pennell & Killip 5978*; *Killip 11260*. Antioquia: *Archer 178, 1007*; *Jervise*. Tolima: *Triana* (type of *C. bella Trianæ*). Cundinamarca: *Pérez 2261, 3007*; *André 1379, 1400, 1519*; *Ariste Joseph A156*. Without locality, *Mutis 3543, 3544, 3546, 4403, 4953, 4975*. Erroneously recorded from Panama.

13. Calliandra diversifolia Britton & Killip, sp. nov.

Ramuli rufo-hirsuto-tomentosi; pinnæ 6–10-jugæ, foliolis 12–18-jugis, oblongis, obtusis, minute ciliolatis, juvenilibus cupreis; capitula ca. 12-flora; calyx campanulatus, parvus, sparse pubescens, dentibus latis, rotundis; corollæ lobi acuti; stamina ca. 20, ad medium conjuncta, tubo longe exserto.

Branchlets rufo-hirsute-tomentose. Stipules linear-lanceolate, up to 6 mm. long; leaf-rachis and petiole 4–10 cm. long, rufo-hirsute-tomentose, at length glabrescent; pinnæ 6–10 pairs, the slender pubescent rachillas 4–8 cm. long; leaflets 12–18 pairs, oblong, 8–14 mm. long, 2–4 mm. wide, obtuse, slightly inequilateral, sparingly pinnate-veined, subchartaceous, minutely ciliolate, when dry the younger copper-colored, the older metallic-green; peduncles hirsutulous or glabrate, 3–6 cm. long; heads about 12-flowered; calyx campanulate, 1.5–3 mm. long, sparingly pubescent, its broad teeth rounded; corolla 6–8 mm. long, hirsutulous, at length glabrate, its 5 ovate-lanceolate lobes acute; stamens about 20, 2.5–3 cm. long, the filaments united about to middle, the tube long-exserted.

Colombia, 1760–1808, *Mutis 441*, type (U.S.), *3542*.

14. Calliandra glomerulata Karst. Fl. Col. 2: 5, *pl. 103*. 1862.

Type locality : Sanaré, Venezuela.
Between Chinácota and La Esmeralda, Norte de Santander, *Killip & Smith 20932.*
Without locality, *Linden 696.* Venezuela.

15. Calliandra flavida Urban, Arkiv. Bot. 24A[4]: 4. 1931.

Type locality : Morne au Camp, Grenada.
Carare, Magdalena Valley, *André 294.* Venezuela ; Grenada ; British Guiana ; and Peru (according to Urban).

16. Calliandra caracasana (Jacq.) Benth. Trans. Linn. Soc. 30: 543. 1875.

Mimosa caracasana Jacq. Coll. 4: 142. 1790.
Anneslia caracasana Britton & Rose, N. Am. Flora 23: 65. 1928.

Type locality : Caracas, Venezuela.
Frequent at middle altitudes in Colombia. Venezuela ; Ecuador ; Haiti (according to Urban).

In all Colombian specimens seen by us the legumes are pubescent.

17. Calliandra tetragona (Willd.) Benth. Journ. Bot. Hook. 2: 139. 1840.

Acacia tetragona Willd. Sp. Pl. 4: 1069. 1806.
Anneslia tetragona Donn. Smith, Enum. Pl. Guat. 1: 10. 1889.

Type locality : Río Guarito, Caracas, Venezuela.
Frequent at lower and middle altitudes in Colombia. Venezuela ; Ecuador ; Panama to Jalisco.

18. Calliandra Toroana Britton & Rose, sp. nov.

Pinnæ 4–7-jugæ, foliolis 15–35-jugis, linearibus, subacutis vel obtusis, costa excentrica; flores capitati, glabri, capitulis numerosis, in paniculis terminalibus; corollæ lobi oblongo-lanceolati, acuti; stamina supra basim conjuncta; legumen lineare, glabrum.

Branches slender, woody, unarmed, glabrous or, when very young, sparingly long-pubescent. Leaves loosely pubescent when unfolding, soon becoming glabrous; stipules triangular-lanceolate, striate, acuminate, 5–7 mm. long; petiole and leaf-rachis 4–8 cm. long; pinnæ 4–7 pairs, 2–5 cm. long; leaflets 15–35 pairs, linear, acutish or obtuse, 4–8 mm. long, about 1 mm. wide, the midvein excentric, the lateral venation obscure; flowers capitate, glabrous; heads numerous in terminal panicles; peduncles about 4 cm. long, or shorter; calyx 2 mm. long, 5-lobed; corolla 5-lobed, the lobes oblong-lanceolate, acute, 4 mm. long; stamens about 10 mm. long, united above the base; legume linear. 7–11 cm. long, 7–8 mm. wide, glabrous, the apex rounded.

Vicinity of Medellín, Antioquia, Colombia, August 18, 1927, *Toro 465*, type (N.Y.).

19. Calliandra marginata Griseb.; R. O. Williams. Fl. Trin. & Tob. 1: 299. 1931.

Calliandra gracilis Klotzsch; Baker in Saund. Ref. Bot. *pl. 294.* 1871. Not Griseb. 1860.

Type locality : Trinidad.
Frequent at lower altitudes in northern Colombia. Trinidad ; Venezuela. VBRANERO.

Calliandra portoricensis (Jacq.) Benth. was erroneously recorded by Bentham from Colombia.

Calliandra Secmannii Benth. has been recorded from Colombia, apparently in error.

17. DUGANDIA Britton & Killip, gen. nov.

Arbor parva ramosissima, vel frutex scandens (?), ramulis inermibus vel spinis remotis crassis recurvatis; foliolis numerosis, parvis, oblongis; flores

spicati; calyx 4–5-dentatus; corolla 4–5-lobata; stamina numerosa, libera; legumen late lineare, planum, curvum, marginibus tenuissimis, undulatis, e corpore transverse septato secedentibus.

A small much-branched tree (or scandent shrub?), the branches with distant stout recurved prickles, or unarmed. Leaves bipinnate, the pinnæ 6–8 pairs, the numerous small linear-oblong leaflets glabrous. Flowers spicate. Calyx 4–5-dentate. Corolla 4–5-lobed. Stamens numerous, free. Legume broadly linear, flat, curved, abruptly beaked, glabrous, its very slender, undulate margins separating from the transversely septate body.

Type species: *Acacia rostrata* H. & B.

1. Dugandia rostrata (H. & B.) Britton & Killip.

Acacia rostrata H. & B.; Willd. Sp. Pl. 4: 1060. 1806.
Mimosa rostrata Poir. in Lam. Encycl. Suppl. 1: 66. 1810.
Mimosa ignava H. B. K. Nov. Gen. & Sp. 6: 259. 1824.
Lysiloma rostrata Benth. Lond. Journ. Bot. 3: 84. 1844.

Type locality: Tropical America (Magdalena River, Colombia, according to H.B K.) Finca de "El Paraíso," Atlántico, *Dugand 529*. San Martín de Loba, Bolívar, *Curran 45*. Tenerife, Magdalena, *Humboldt & Bonpland* (co-type). Endemic. BARANOA.

18. VACHELLIA Wight & Arn. Prodr. 272. 1834.

Type species: *Acacia Farnesiana* Willd.

1. Vachellia Farnesiana (L.) Wight & Arn. Prodr. 272. 1834.

Mimosa Farnesiana L. Sp. Pl. 521. 1753.
Acacia Farnesiana Willd. Sp. Pl. 4: 1083. 1806.

Type locality: Domingo.
Frequent in northern Colombia. Venezuela to Argentina; Panama to Sonora and Lower California; West Indies; southeastern United States. UÑA DD CABRA, PELÁ, CUJI CIMARRON, AROMO.

19. MYRMECODENDRON Britton & Rose, N. Am. Flora 23: 91. 1928.

Type species: *Acacia Hindsii* Benth.

1. Myrmecodendron costaricense (Schenck) Britton & Rose, N. Am. Flora 23: 93. 1928.

Acacia costaricensis Schenck, Repert. Sp. Nov. Fedde 12: 361. 1913.

Type locality: Near Lagasto, Costa Rica.
Dept. Altántico, *Elias 245, 479, 1070; Niemeyer 209; Dugand 117b*. Dept. Bolívar, *Heriberto 39*. Río Sinú, Bolívar, *Humboldt & Bonpland*, cited as *Acacia cornigera*. Santa Marta, *Purdie*, cited by Bentham as *Acacia spadicigera*. Mexico to northern Colombia. CORNIZUELO, CACHITOS, CASA DD HORMIGAS.

20. POPONAX Raf. Sylva Tell. 118. 1838.

Type species: *Mimosa tortuosa* L.

KEY TO SPECIES OF POPONAX

Legume 1.5–2 cm. broad; young twigs yellowish lanate.   1. *P. Pennatula.*
Legume (unknown in No. 4) much narrower.
    Legume turgid, little compressed, more or less
      constricted ....   2. *P. tortuosa.*
    Legume flattened.
      Pinnæ 8–17 pairs; leaflets 1-veined, or lateral
      venation obscure.
        Twigs and inflorescence sparingly pubes-
        cent ....   3. *P. flexuosa.*
        Twigs and inflorescence densely canes-
        cent ....   4. *P. canescens.*

Pinnæ only 2 or 3 pairs; leaflets pinnately
veined .... 5. *P. venosa.*

1. **Poponax Pennatula** (Schl. & Cham.) Britton & Rose, N. Am. Flora 23: 88.
1928.

Inga Pennatula Schl. & Cham. Linnæa 5: 593. 1830.
Acacia Pennatula Benth. Lond. Journ. Bot. 1: 390. 1842.

Type locality: Hacienda de la Laguna, Veracruz, Mexico.
La Palla, El Valle, *André 3570.* El Salvador to Sinaloa and Tamaulipas.

2. **Poponax tortuosa** (L.) Raf. Sylva Tell. 118. 1838.

Mimosa tortuosa L. Syst. Nat. ed. 10, 1312. 1759.
Acacia tortuosa Willd. Sp. Pl. 4: 1083. 1806.

Type locality: Jamaica.
Frequent in northern Colombia. Curaçao; Aruba; Bonaire; Jamaica; Virgin Islands
and Lesser Antilles, south to Martinique. AROMO.

3. **Poponax flexuosa** (H. & B.) Britton & Rose.

Acacia flexuosa H. & B.; Willd. Sp. Pl. 4: 1080. 1806.
Mimosa flexuosa Poir. in Lam. Encycl. Suppl. 1: 79. 1810.

Type locality: Cumaná, Venezuela.
Santa Marta, Magdalena, *H. H. Smith 41; Killip & Smith 21093.* Bolívar, *Killip &
Smith 14090; Heribcrto 383.* Venezuela; French Guiana.

Our identification of this species is not wholly satisfactory, based on de-
scription, and on a photograph of the incomplete type specimen in the her-
barium of the Paris Museum.

Acacia macracantha H. & B., which has been recorded as having wide range
in tropical America, is definitely known to us only from Ecuador and Peru;
it is well illustrated by Kunth, Mim. *plate 28.*

4. **Poponax canescens** Britton, sp. nov.

Ramuli foliorum rachis inflorescentiaque dense canescentia; spinæ stipu-
lares aciculares, canescentes; glandula prope basim petiolorum, etiam inter
juga aliqua pinnarum; pinnæ 8–17-jugæ, foliolis 30–40-jugis, linearibus, obtusis,
demum glabris; pedunculi fasciculati; corollæ lobi ovato-lanceolati, acuti;
stamina prope basim conjuncta.

Twigs, leaf-rachis and inflorescence densely canescent. Stipular spines
acicular, about 2 cm. long, or shorter, also canescent, at least when young;
leaves 8–13 cm. long, the slender petiole 2–6 cm. long, bearing near the base
an oblong, sessile, nearly flat gland about 2 mm. long; leaf-rachis slender,
bearing a small orbicular gland between some of the pairs of pinnæ; pinnæ
8–17 pairs, the canescent or short-pubescent rachillas 2–3 cm. long; leaflets
30–40 pairs, linear, obtuse, 2.5–3 mm. long, about 0.7 mm. wide, 1-veined, glabrous
when old; peduncles several at the nodes, about 15 mm. long, or shorter; flowers
in dense canescent globose heads; calyx 1 mm. long, 5-toothed; corolla about
2 mm. long, its 5 lobes ovate-lanceolate, acute; stamens many, a little longer
than the corolla, united near the base.

Anapoima, Cundinamarca, Colombia, 400 m. altitude, *Triana 4489,* type (N.Y.);
Ariste Joseph. Tocaima, Cundinamarca, *Pérez 2058.* CHUCUNCHA, AMBUCA, AMBUQUE.

5. **Poponax (?) venosa** Britton, sp. nov.

Petioli et rachides laxe brevipubescentia; pinnæ 2–3-jugæ, foliolis 10–14-
jugis, anguste oblongis, glabris, subchartaceis, subtus valde penniveniis, costa
subexcentrica; pedunculi solitarii vel bini, breviter villosi; flores glabri; calycis
dentes ovati; corollæ lobi lanceolati, acuti; stamina libera; legumen lineare,
glabrum.

Twigs apparently very short. Leaves clustered, the petiole and rachis only 1–2 cm. long, loosely short-pubescent, the petioles (at least some of them) bearing a minute orbicular sessile gland below the lower pair of pinnæ; pinnæ 2 or 3 pairs, 1–2 cm. long, the slender rachilla short-pubescent; leaflets 10–14 pairs, narrowly oblong, 3–4 mm. long, 1 mm. wide, acute or obtuse, glabrous, subchartaceous, nearly smooth above, strongly and irregularly pinnate-veined beneath, the midvein nearly central; peduncles solitary or 2-together, densely short-villous, about 10 mm. long; heads globose, many-flowered; flowers glabrous; calyx 2 mm. long, its teeth ovate; corolla 3 mm. long, its lanceolate lobes acute; stamens many, distinct, about 4 mm. long; young legume linear, glabrous, flat, 3 cm. long, narrowed toward the base, obliquely short-beaked.

Vicinity of Medellín, Antioquia, Colombia, August 20, 1927, *Toro 478*, type (N.Y.).

21. ACACIELLA Britton & Rose, N. Am. Flora 23 : 96. 1928.
Type species : *Acacia villosa* Sw.

KEY TO SPECIES OF ACACIELLA
Glabrous, puberulent, or sparingly short-pubescent.
    Legume broadly linear, cuneate at base, up to
        9 cm. long .... 1. *A. santandcrensis.*
    Legume oblong, rounded at base, 4–5.5 cm. long. 2. *A. martensis.*
Villous, legume linear-oblong, the base narrowed.. 3. *A. Holtonii.*

1. Acaciella santanderensis Britton & Killip, sp. nov.

Frutex ; foliorum rachides et rachillæ sparse brevipubescentes ; pinnæ 8–16-jugæ, foliolis 20–40-jugis, linearibus, acutis, subchartaceis, glabris vel sparse ciliolatis, costa excentrica ; paniculæ axillares ; legumen glabrum, 5–8-spermum, ad basim cuneatum.

A shrub, 6–12 dm. high, the stem sparingly short-pubescent when young, becoming glabrous. Leaves 12–17 cm. long, the rachis and rachillas sparingly short-pubescent; pinnæ 8–16 pairs, 5–7 cm. long; leaflets 20–40 pairs, linear, acute, glabrous or sparingly ciliolate, 1-veined, 3–6 mm. long, subchartaceous, the vein excentric; panicles axillary, about as long as the leaves, or shorter, in fruit glabrate; peduncles relatively stout, 1.5–2 cm. long; legume broadly linear, glabrous, 9 cm. long, or shorter, 12–15 mm. wide, 5–8-seeded, the base cuneate, the apex acute or obtuse.

Open hillside, between Pamplona and La Isla, Norte de Santander, Colombia, 2000–2500 m. altitude, February 27, 1927, *Killip & Smith 19791*, type (N.Y.). Río Suratá Valley, Santander, *Killip & Smith 16392, 16457.*

2. Acaciella martensis Britton & Killip, sp. nov.

Caulis puberulus ; pinnæ ca. 16-jugæ, foliolis 20–40-jugis, anguste linearibus, acutis, glabris, 1-veniis, costa excentrica ; pedunculi glabri ; legumen oblongum, ad basim rotundum, 5–8-spermum, glabrum.

Stem puberulent. Leaves about 15 cm. long, the rachis and rachillas puberulent; pinnæ about 16 pairs, about 6 cm. long, or shorter ; leaflets 20–40 pairs, narrowly linear, acute, 1-veined, glabrous, about 3 mm. long, the vein excentric; fruiting panicle longer than the subtending leaf; peduncles 12–15 mm. long, glabrate ; legume oblong, glabrous, 4–4.5 cm. long, 12–15 mm. wide, rounded at base, normally obtuse or rounded at apex, 5–8-seeded.

Onaca, Santa Marta, Magdalena, Colombia, about 700 m. elevation, February 7, 1899, *H. H. Smith 295a*, type (N.Y.).

3. Acaciella Holtonii Britton & Killip, sp. nov.

Frutex vel arbor, caule petiolis rachidibus, rachillis paniculaque villosis ; pinnæ 12–17-jugæ, foliolis 20–40-jugis, linearibus, acutis, glabris, 1-veniis, cilio-

latis, costa subexcentrica; corolla glabra, lobis oblongo-lanceolatis, acutis; legumen lineari-oblongum, glabrum, ad basim angustatum.

A shrub or tree, about 6 m. high, or lower, the stem simple, or little branched, villous, at least above. Leaves 10–20 cm. long, the petiole, rachis and rachillas villous; pinnæ 12–17 pairs, 3–6 cm. long; leaflets 20–40 pairs, linear, acute, glabrous, ciliolate, 1-veined, about 3 mm. long, the vein slightly excentric; panicles axillary, villous, sometimes much elongated and twice as long as the leaves; heads numerous, globose; peduncles very slender, about 2 cm. long, or shorter; corolla glabrous, the lobes oblong-lanceolate, acute, 2 mm. long; stamens numerous, distinct, 4–5 mm. long; legume linear-oblong, 4–7 cm. long, 9–12 mm. wide, glabrous, apiculate, 5–8-seeded, the base narrowed.

La Paila, El Valle, Colombia, May 30, 1853, *Holton 998*, type (N.Y.), *997*. Santa Marta, *H. H. Smith 295; Seifriz 600*. Bucaramanga, Santander, *Killip & Smith 16296*. Medellín, *Archer 775; Daniel 43; Toro 164, 406, 576*. Popayán, *Lehmann 5369, B. T. 373*. Without locality, *Mutis 4400*. Colombian specimens at Kew referred by Bentham to *Acacia filicina* prove to belong to *Acaciella Holtoni*. CARBONERO.

22. SENEGALIA Raf. Sylva Tell. 119. 1838.

Type species: *Mimosa Senegal* L.

KEY TO SPECIES OF SENEGALIA

<pre>
A. Stipules and bracts large, foliaceous, ovate...... 1. S. tamarindifolia.
B. Stipules and bracts inconspicuous, or none
   1. Twigs and foliage without prickles.
      a. Leaves and branches glabrous or pubescent.
         Leaflets oblong or oblong-lanceolate,
            sometimes subfalcate .... 2. S. glomerosa.
         Leaflets linear to lanceolate, narrower.
            Leaflets puberulent or glabrous;
               legume glabrous.
                  Legume broadly linear, 2–3 cm.
                     wide .... 3. S. polyphylla.
                  Legume linear, narrower.
                     Legume 6–7 cm. long, 1.5 cm.
                        wide; leaflets linear..... 4. S. Guacamayo.
                     Legume 12–17 cm. long, 2
                        cm. wide; leaflets lance-
                        olate .... 5. S. lobana.
            Leaflets pilose; legume puberulent. 6. S. cundinamarcæ.
      b. Petioles and branches densely villous;
            flowers glabrous .... 7. S. popayana.
   2. Twigs and foliage more or less prickly.
      a. Trees or upright shrubs.
         *Prickles recurved.
            Leaflets glabrous.
               Heads very small, few-flowered;
                  leaflets about 2 mm. long.... 8. S. cordobana.
               Heads larger, several-flowered;
                  leaflets 3–4 mm. long....... 9. S. riparia.
            Leaflets pubescent, at least beneath;
               legume pubescent.
                  Legume obtuse at base, 15–22
                     mm. wide; leaflets densely
                     pubescent .... 10. S. huilana.
                  Legume narrowed at base, 12–18
                     mm. wide; leaflets not densely
                     pubescent.
                        Leaflets about 1.5 mm. wide.
                           loosely pilose beneath.... 11. S. affinis.
</pre>

> Leaflets about 2.5 mm. wide,
> appressed-pubescent be-
> neath .... 12. *S. Eliasiana.*
> **Prickles spreading or erect, straight. 13. *S. Lehmannii.*
> b. Vines or scandent shrubs.
> Glands of petiole and rachis sessile.
> Twigs, rachis and inflorescence
> densely tomentulose .... 14. *S. tomentella.*
> Foliage glabrous; inflorescence un-
> known .... 15. *S. turbacensis.*
> Petiole and rachis bearing stout-stalked
> glands .... 16. *S. podadenia.*

1. **Senegalia tamarindifolia** (L.) Britton & Rose, N. Am. Flora 23: 120. 1928.

Mimosa tamarindifolia L. Sp. Pl. 523. 1753.
Acacia tamarindifolia Willd. Sp. Pl. 4: 1092. 1806.

Type locality: Tropical America.
Santa Marta, *H. H. Smith* 3½, 2247. Dibulla, Magdalena, *Seifriz 222.* Barran-
quilla, *Elias 412.* Cartagena, *Ariste Joseph.* Venezuela; Guadeloupe; Martinique.

2. **Senegalia glomerosa** (Benth.) Britton & Rose, N. Am. Flora 23: 116. 1928.

Acacia glomerosa Benth. Lond. Journ. Bot. 1: 521. 1842.

Type locality: Rio de Janeiro, Brazil.
Santa Marta, *H. H. Smith 39, 29½.* Barranquilla, *Elias 267, 998.* Bogotá, Cundina-
marca, *Triana ½½7.* Without locality, *Mutis 3536.* Venezuela; Guiana (according to
Bentham); Brazil; El Salvador to Yucatán. MULATO, BARANOA.

3. **Senegalia polyphylla** (DC.) Britton & Rose.

Acacia polyphylla DC. Cat. Hort. Monsp. 74. 1813.

Type locality: Santa Marta, Colombia.
Santa Marta. *H. H. Smith 293, 926.* Goajira Peninsula, *Dawe 583.* Cartagena,
Heriberto 29½, 320. El Humbo, Boyacá, *Lawrance ½50.* Venezuela; Brazil.

4. **Senegalia Guacamayo** Britton & Killip, sp. nov.

Arbor inermis, glabra, petiolis rachidibus rachillisque puberulis exceptis;
glandula petiolorum subelevata, concava; rachis inter pinnas superiores glan-
dulifera, glandulis minutis, orbiculatis; pinnæ 6–10-jugæ, foliolis 30–50-jugis,
linearibus, acutis vel subacutis, supra nitidis, costa valde excentrica; flores
capitati; legumen anguste lineare, planum.

A tree, the trunk about 7 dm. in diameter, the twigs glabrous, unarmed.
Petiole and rachis about 10 cm. long, or shorter, puberulent, slender, the
petiole bearing a sessile, somewhat elevated, concave gland about 1 mm. in
diameter, the rachis bearing minute orbicular glands between the upper pinnæ;
pinnæ 6–10 pairs, the slender puberulent rachilla 5–7 cm. long; leaflets 30–50
pairs, linear, glabrous, closely approximate, acute or acutish, 5–7 mm. long, or
the upper ones shorter, about 1 mm. wide, shining above, dull beneath, the
delicate midvein very excentric, the lateral venation wholly obscure, the base
subtruncate; fruiting peduncle glabrous, about 5 cm. long; flowers capitate;
legume linear, flat, glabrous, dull, irregularly transverse-veined, 6–7 cm. long,
about 1.5 cm. wide, the apex apiculate, the base rather abruptly narrowed into
a short stipe, the narrow margins slightly elevated.

Prado, Santa Marta, Magdalena, Colombia, January 13, 1930, *Record 7,* type (N.Y.).
GUACAMAYO.

5. **Senegalia lobana** Britton & Killip, sp. nov.

Arbor inermis; petioli eglandulosi, rachis eglandulosa (?) puberula; pinnæ
8–15-jugæ, foliolis 12–25-jugis, lanceolatis vel oblongo-lanceolatis, acutis, supra

glabris, subtus appresso-puberulis, costa valde excentrica; legumen lineare, chartaceum, glabrum, obtuse apiculatum.

A tree about 15 m. high, the twigs and leaves unarmed. Petioles 3–4 cm. long, glandless; rachis slender, puberulent, 6–12 cm. long, apparently also glandless; pinnæ 8–15 pairs, the nearly filiform rachilla 2–5 cm. long; leaflets 12–25 pairs, lanceolate to oblong-lanceolate, oblique, acute, 4–5 mm. long, about 1.5 mm. wide, glabrate above, appressed-puberulent beneath, the midvein very excentric, the base truncate; fruiting peduncles about 1 cm. long; legume linear, chartaceous, glabrous, 12–17 cm. long, 2 cm. wide, longitudinally dehiscent, bluntly apiculate, the cuneate base narrowed into a stipe about 1 cm. long; seeds suborbicular, flat, shining 5–8 mm. long.

San Martín de Loba, Bolívar, Colombia, April-May, 1916, *H. M. Curran 55*, type (U.S.).

6. Senegalia cundinamarcæ Britton & Killip, sp. nov.

Arbor inermis (?), ramulis petiolis rachidibusque dense puberulis, glandulis petiolorum 1–2, convexis; pinnæ 6–12-jugæ, rachilla brevipubescente, foliolis 15–30-jugis, linearibus, obtusis. dense longipubescentibus, costa excentrica; flores capitati, puberuli, capitulis paniculatis; corollæ lobi ovati, acuti; legumen lineari-oblongum, planum, dense puberulum.

A tree, apparently unarmed, the slender twigs densely puberulent. Petiole and leaf-rachis puberulent, 5–10 cm. long; petiole bearing 1 or 2, sessile, convex glands about 1 mm. in diameter, or smaller; pinnæ 6–12 pairs, 2–4 cm. long, the nearly filiform rachilla short-pubescent; leaflets 15–30 pairs. linear, obtuse, 3–6 mm. long, about 1 mm. wide, densely long-pubescent on both sides, pinnately veined, the midvein excentric; heads globose, numerous, panicled; peduncles slender, short-pilose, about 2 cm. long, or shorter; flowers puberulent; calyx 1.5 mm. long, with ovate acute teeth; corolla 3 mm. long, with ovate acute lobes; stamens many, distinct, 6–7 mm. long; legume linear-oblong, flat, densely puberulent, abruptly short-tipped, 8–11 cm. long, 2–2.5 cm. wide, narrowed at base, its slender stipe about 10 mm. long.

Dept. Cundinamarca, Colombia. Girardot, 350–400 m. altitude, July 19, 1914, *Rusby & Pennell 133*, type (N.Y.). Partillo, 450–500 m. altitude, August 14, 1917, *Rusby & Pennell 1346*.

7. Senegalia popayana Britton & Killip, sp. nov.

Inermis; ramuli petioli foliorum rachides inflorescentiaque dense villosa; petioli et rachides eglandulosa (?); pinnæ ca. 10-jugæ, foliolis 40–50-jugis, linearibus, acutis, 1-veniis, juvenilibus ciliatis; capitula parva, paniculata, pedunculis villosis; flores glabri; calycis dentes breves, lati; corollæ lobi ovati, acuti.

Unarmed, the twigs, petioles, leaf-rachises and inflorescence densely long-villous. Petiole and rachis about 13 cm. long, or shorter, apparently eglandular; pinnæ about 10 pairs, 5–7 cm. long, the rachilla villous; leaflets 40–50 pairs, linear, acute, 1-veined, ciliate when young, 4–6 mm. long, about 1 mm. wide; heads small, panicled; peduncles villous, about 10 mm. long, or shorter; bracts narrowly linear, fugacious, 4–5 mm. long; flowers glabrous; calyx 1 mm. long, with short broad teeth; corolla 2 mm. long, its lobes ovate, acute; stamens about 4 mm. long, numerous, distinct.

Popayán, El Cauca, Colombia, 1818 m. altitude, April 17, 1876, *André 2773*, type (N.Y.). Without locality, *Triana.*

8. Senegalia cordobana Britton & Killip, sp. nov.

Frutex, ramulis dense puberulis, aculeis brevibus remotis reflexis armatis; petioli et rachides dense puherula, glandulis orbiculatis, concavis; pinnæ 10–22-jugæ, foliolis 30–40-jugis, linearibus, obtusis, glabris, 1-nerviis; inflorescentia laxe paniculata, puberula, capitulis parvis, globosis.

A shrub, about 3 m. high, the slender, densely puberulent twigs armed with short distant reflexed prickles. Leaves 6–8 mm. long, the slender petiole and rachis densely puberulent; petiole bearing an orbicular sessile concave gland about 1 mm. in diameter; rachis bearing a similar smaller gland between the upper pairs of pinnæ; pinnæ 10–22 pairs, 2–3 cm. long, the very slender rachilla glabrate; leaflets 30–40 pairs, linear, glabrous, obtuse, 2–3 mm. long, about 0.5 mm. wide, delicately 1-nerved; inflorescence loosely paniculate, its slender branches puberulent, 6–10 cm. long; heads small, globose; peduncles only 6 mm. long, or shorter; flowers white, puberulent; calyx about 1 mm. long, its teeth short and broad; corolla 2 mm. long, its ovate lobes acute; stamens about 4 mm. long, nearly distinct.

Cliffs along Río Dagua, Córdoba, El Valle, Colombia, 80–100 m. altitude, October 9, 1922, *Killip 11771*, type (N.Y.).

9. Senegalia riparia (H. B. K.) Britton & Rose.

Acacia riparia H. B. K. Nov. Gen. & Sp. **6**: 276. 1824.

Type locality: Junction of the Amazon and Chamaya rivers, Jaen de Bracamoras, Peru.

Fusagasugá, Cundinamarca, *André 1446; Triana*. Without locality, *Mutis 4976*, both determined from description. Peru; Brazil; Guiana (according to Bentham). Climbing West Indian vines referred by authors to this species are manifestly distinct. Doubtfully this species are *Mutis 3538* and *3626*, and a specimen from Villavicencio, collected by Nicéforo. RASGA, RASGA-RASGA, PANELO, TOLDILLO.

10. Senegalia huilana Britton & Killip, sp. nov.

Arbor, ramulis aculeatis, juvenilibus puberulis, aculeis recurvis; petiolus rachisque puberula, plerumque inermia, glandulis petiolorum oblongis, eis rachidis orbicularibus; pinnæ 6–10-jugæ, foliolis 15–35-jugis, lineari-oblongis, obtusis, supra brevipubescentibus, subtus villosis, trinerviis, costa excentrica; capitula globosa, in paniculis terminalibus; calyx minute puberulus; legumen late lineare, planum, dense puberulum, ad basim obtusum.

A tree, with slender, prickly twigs, finely puberulent when young, the prickles recurved, 2–3 mm. long. Petiole and leaf-rachis slender, puberulent, 6–9 cm. long, unarmed, or with an occasional prickle; petiole bearing an oblong sessile concave gland about 2 mm. long, rachis bearing a smaller orbicular concave gland between the upper pinnæ or also between the lower pair; pinnæ 6–10 pairs; rachilla very slender, pubescent, 4–6 cm. long; leaflets 15–35 pairs, linear-oblong, thin, obtuse, 4–7 mm. long, about 1.5 mm. wide, short-pubescent above, villous beneath, 3-nerved at base, pinnately few-veined, the midvein excentric; heads globose, many-flowered, numerous in terminal panicles; peduncles short-pubescent, 6–10 mm. long; calyx minutely puberulent, 1.5 mm. long, with ovate acute teeth; corolla 2.5 mm. long, its lobes ovate, acute; stamens many, distinct, 5–6 mm. long; legume broadly linear, flat, densely puberulent, abruptly tipped, obtuse at base, 8–10 cm. long, 1.5–2.2 cm. wide, with narrow, slightly elevated margins, longitudinally dehiscent, the valves chartaceous; seeds 8–10, orbicular, compressed, black, about 6 mm. broad.

Between Río Cabrera and Villavieja, Huila, Colombia, July 26, 1917, 500–550 m altitude, *Rusby & Pennell 365*, type (flowers, N.Y.); same locality and date *Rusby & Pennell 378* (fruit).

11. Senegalia affinis Britton & Killip, sp. nov.

Frutex grandis, ramulis puberulis, aculeis sparsis recurvis; petioli glandula orbiculata; pinnæ 6–9-jugæ, foliolis 20–35-jugis, linearibus, obtusis, membranaceis, supra glabris, subtus laxe pilosis, costa subcentrale; legumen lineare, dense puberulum, ad basim angustatum.

A large shrub, the slender puberulent twigs sparingly prickly, the recurved prickles about 3 mm. long. Petiole 1.5–2 cm. long, bearing a slightly elevated, orbicular gland about 0.5 mm. in diameter; leaf-rachis slender, glabrate, 4–6

cm. long; pinnæ 6-9 pairs, the very slender, short-pubescent rachillæ 3-5 cm. long; leaflets 20-35 pairs, linear, obtuse, membranous, 4-6 mm. long, about 1.5 mm. wide, glabrate above, loosely pilose beneath, the midvein nearly central, the lateral venation rather strong; legume linear, densely puberulent, longitudinally dehiscent, 8-12 cm. long, 12-18 mm. wide, the apex acutish or obtuse, short-tipped, the base narrowed or cuneate, the chartaceous valves with narrow thickened margins.

Guamacito, Santa Marta, Magdalena, January 15, 1930, *S. J. Record ?1*, type (N.Y.).

12. Senegalia Eliasiana Britton & Killip, sp. nov.

Rami sparse aculeati, aculeis recurvis, ramulis dense puberulis; folii glandulæ orbiculatæ; pinnæ numerosæ, foliolis 12-25-jugis, linearibus, obtusis, supra glabris, subtus appresso-pubescentibus, costa subexcentrica; inflorescentia terminalis, paniculata, pedunculis fasciculatis, dense puberulis, capitulis globosis; calyx 4-dentatus, puberulus; corolla glabra; legumen lineare, planum, pubescens, ad basim angustatum.

Branches bearing an occasional recurved prickle, the slender young twigs densely puberulent. Petiole and rachis slender, 6-12 cm. long; petiole bearing a sessile orbicular gland about 1 mm. in diameter; rachis sparingly prickly and bearing a smaller similar gland between the lower and upper pairs of pinnæ; pinnæ several-many pairs; rachilla filiform, puberulent, about 6 cm. long, or shorter; leaflets 12-25 pairs, linear, obtuse, 8-10 mm. long, about 2 mm. wide, appressed-pubescent beneath, glabrous above, the midvein somewhat excentric, the base truncate, the lateral venation not prominent; inflorescence a terminal panicle; peduncles clustered, densely puberulent, about 16 mm. long, or shorter; heads globose, many-flowered; calyx minutely puberulent, 4-toothed, 2 mm. long, the teeth ovate; corolla 5-lobed, glabrous, about 3 mm. long, the lobes ovate; stamens many, 5-6 mm. long; legume linear, pubescent, flat, 10-12 cm. long, about 18 mm. wide, the base narrowed or cuneate, the stipe about 10 mm. long.

Baranoa, Barranquilla, Atlántico, Colombia, November. 1928, *Elias 602*, type (U.S.).

13. Senegalia Lehmannii Britton & Killip, sp. nov.

Arbor, ramulis aculeis rectis ascendentibus vel divaricatis armatis, juvenilibus dense brevipilosis; pinnæ 6-10-jugæ, foliolis linearibus, subacutis, dense pubescentibus, demum glabratis, costa fere centrale; capitula globosa, axillaria, in racemis brevibus terminalibus; flores glabri; calyx subtruncatus, minute 5-dentatus; corolla alte 5-lobata.

A tree about 5 m. high, the twigs densely short-pilose when young, armed with straight, ascending or spreading, broad-based prickles 2-3 mm. long. Young leaves 4-6 cm. long, the very slender petiole and rachis short-pilose; pinnæ 6-10 pairs, the short rachillæ nearly filiform; leaflets 15-25 pairs, linear, acutish, 1.5-2.5 mm. long, densely pubescent when young, becoming glabrate, the delicate midvein nearly central; heads globose, several-many-flowered, axillary, and in short terminal racemes; peduncles very slender, short-pilose, 1-2 cm. long; flowers glabrous; calyx about 1 mm. long, nearly truncate, minutely 5-toothed; corolla 3 mm. long, deeply 5-lobed; stamens about 4.5 mm. long.

El Cauca, Colombia, August 28, 1881. *Lehmann 924*, type (U.S.). This collection has been cited as *Acacia adhaerens* Benth. by Micheli. GUARANGO.

14. Senegalia tomentella Britton & Killip, sp. nov.

Caulis scandens, dense tomentella, foliolis floribusque exceptis, ramulis aculeis brevibus recurvis armatis; glandulæ petioli et rachidis sessiles; pinnæ 12-25-jugæ, foliolis 20-45-jugis, linearibus, subacutis, glabris, costa excentrica; panicula terminalis laxa, capitulis globosis; flores glabri; calyx 5-dentatus; corolla 5-lobata, calyce paullo longior.

A vine, the twigs, petioles, leaf-rachis and inflorescence densely tomentulose, the twigs armed with short recurved prickles. Petioles slender, about 5 cm. long, bearing a sessile oblong gland; rachis 9–16 cm. long, bearing sessile glands between the upper pairs of pinnæ; pinnæ 12–25 pairs, 3–4.5 cm. long; leaflets 20–45 pairs, linear, glabrous, 2.5–3 mm. long, nearly 1 mm. wide, acutish, the base obliquely truncate, the midvein excentric, the lateral venation obscure; inflorescence a terminal loose panicle about 25 cm. long, or shorter; heads globose, numerous, few-several-flowered, about 8 mm. in diameter; flowers glabrous; calyx 5-toothed, 1.2 mm. long; corolla 5-lobed, a little longer than the calyx; stamens 3–4 mm. long.

Forest, Río Putumayo, at the Colombia-Peru boundary, September 26-October 10, 1930, *G. Klug 1651,* type (N.Y.).

15. Senegalia turbacensis Britton & Killip, sp. nov.

Frutex subscandens, caule glabro, aculeis recurvis armato; petiolus et rachis puberula vel glabrata, rachide sparse aculeata; petioli prope basim appendice sessile oblonga plana donati, glandulis rachidis orbiculatis, sessilibus; pinnæ ca. 30-jugæ, foliolis 20–50-jugis, linearibus, subacutis, glabris, costa submarginale.

A subscandent shrub, up to about 3 m. long, the slender glabrous stem armed with recurved prickles about 2 mm. long. Leaves distant, the slender, puberulent or glabrate petiole and rachis sparingly prickly, 15–20 cm. long; petiole about 2 cm. long, bearing near the base a flat sessile oblong appendage 3 or 4 mm. long; rachis bearing between the upper pairs of pinnæ an orbicular concave sessile gland nearly 1 mm. broad; pinnæ about 30 pairs, 2–4 cm. long, the very slender rachilla glabrous; leaflets 20–50 pairs, linear, approximate, about 2.5 mm. long, 0.5 mm. wide, glabrous, acutish, the midvein nearly marginal, the lateral venation obscure.

Thicket, vicinity of Turbaco, Bolívar, Colombia, 200–300 m. altitude, November 14, 1926, *Killip & Smith 14482,* type (N.Y.).

The flowers, not seen, were said to be white. ZARZA REDONDA.

16. Senegalia podadenia Britton & Killip, Phytologia 1: 24. 1933.

Type locality: Mt. Chapón region, western Boyacá, Colombia.
Mt. Chapón, Boyacá, *Lawrance 346* (type).

23. LEUCÆNA Benth. Journ. Bot. Hook. 4: 416. 1842.

Type species: *Mimosa glauca* L.

KEY TO SPECIES OF LEUCÆNA

Leaflets 10–20 pairs, linear to lanceolate, 8–15 mm.
long .... 1. *L. glauca.*
Leaflets 3–6 pairs, ovate to elliptic, 1–4 cm. long.
   Plant glabrous throughout; heads in axillary
     fascicles .... 2. *L. colombiana.*
   Plant with the twigs, leaves and inflorescence
     pubescent; heads racemose. .... 3. *L. bolivarensis.*

1. Leucæna glauca (L.) Benth. Journ. Bot. Hook. 4: 416. 1842.

Mimosa glauca L. Sp. Pl. 520. 1753.

Type locality: America.
Apparently uncommon in Colombia; Medellín, *Archer 732, 872.* La Plata, Tolima, *Lehmann 2268.* Tocaima, Cundinamarca, *Pérez 2238.* French Guiana to Venezuela, Brazil and Chile; West Indies, north to Florida and Bermuda; Panama to Veracruz. Old World tropics. PANELO.

2. Leucæna colombiana Britton & Rose, sp. nov.

Frutex vel arbor ubique glabra; petioli glandula conica, parum infra jugum inferius pinnarum: pinnæ 2-jugæ, foliolis 3–4-jugis, ovatis vel lanceo-

latis vel (supremis) obovatis, acutis, membranaceis; capitula axillaria, fasciculata; petala lineari-spathulata, acuta.

A shrub, or a tree up to about 15 m. high, glabrous throughout. the twigs slender. Leaves about 15 cm. long: pinnæ 2 pairs; petiolar gland low-conic, borne a little below the lower pair of pinnæ; pinnæ 2 pairs; leaflets 3 or 4 pairs, membranous, sharply acute, 2.5–7 cm. long, ovate, lanceolate, or the upper pair obovate; heads in axillary fascicles shorter than the petioles, the peduncles about 15 mm. long, or shorter; bractlets ciliolate; calyx 5-toothed, about 1 mm. long; petals linear-spatulate, acute, 1.5 mm. long; stamens about 4 mm. long, distinct.

Santa Marta, Magdalena, Colombia. Type from forest, north of Bonda, October 22, 1898, *H. H. Smith 37a*, type (N.Y.), *37*.

3. Leucæna bolivarensis Britton & Killip, sp. nov.

Arbor parva, ubique brevipubescens floribus exceptis; glandula conica, prope medium petioli; pinnæ 2–3-jugæ, foliolis 5–6-jugis, subchartaceis, acutis, supremis elliptico-obovatis, ceteris ovato-ellipticis; capitula racemosa in ramis quam foliis brevioribus; petala glabra.

A small tree, about 4 m. high, the twigs, leaf-rachis and inflorescence rather densely short-pubescent. Leaves about 12 cm. long; pinnæ 2 or 3 pairs; gland low-conic, borne near the middle of the petiole; leaflets 5 or 6 pairs, subchartaceous, acute, loosely short-pubescent on both sides, 1–3 cm. long, the upper pair elliptic-obovate, the others ovate-elliptic; inflorescence shorter than the leaves, the branches densely pubescent, the heads few or several, racemose on peduncles about 15 mm. long, or shorter; calyx about 1 mm. long, minutely puberulous toward apex; petals oblong-lanceolate, about 1.5 mm. long, acute, glabrous; stamens about 3.5 mm. long.

Torrecilla, near Turbaco, Bolívar, Colombia, 150–300 m. altitude, edge of woods, November 7, 1926, *Killip & Smith 14289*, type (N.Y.). VERANIBO.

24. DESMANTHUS Willd. Sp. Pl. 4: 1044. 1806.

[ACUAN Medic. Theod. 62. 1786.]

Type species: *Mimosa virgata* L.

KEY TO SPECIES OF DESMANTHUS

Leaf-rachis bearing a gland between only the lowest
    pair of pinnæ.
    Gland elliptic, 1.2–2 mm. long; plant erect...... 1. *D. virgatus.*
    Gland orbicular, smaller.
        Legume 4–5 mm. wide; plant erect........ 2. *D. latus.*
        Legume 2–3 mm. wide; plant diffuse........ 3. *D. depressus.*
Leaf-rachis (at least of some leaves) bearing orbicular glands between each pair of pinnæ; legume
    dimorphic .... 4. *D. multiglandulosus.*

1. Desmanthus virgatus (L.) Willd. Sp. Pl. 4: 1047. 1806.

Mimosa virgata L. Sp. Pl. 519. 1753.

Acuan virgatum Medic. Theod. 62. 1786.

Type locality: East Indies.
Frequent or common in Colombia. Tropical and subtropical America, north to Florida, Bermuda, and Morelos. Tropical Asia.

2. Desmanthus latus Killip.

Acuan latum Britton & Rose, N. Am. Flora 23: 132. 1928.

Type locality: Panama.
Labateca, Norte de Santander, *Killip & Smith 20535*. Panama; El Salvador; Veracruz.

3. **Desmanthus depressus** H. & B ; Willd. Sp. Pl. 4: 1046. 1806.

Acuan depressum Kuntze, Rev. Gen. 158. 1891.

Type locality : South America.
Frequent in northern Colombia.   Tropical and subtropical America, north to Florida and Texas.

4. **Desmanthus multiglandulosus** Britton & Killip, sp. nov.

Glaber, foliis juvenilibus sparse pubescentibus vel ciliolatis exceptis; foliorum aliquorum rachis inter jugum quodque pinnarum glandulosa, glandula orbiculata ; pinnæ 4–7-jugæ, foliolis 12–25-jugis, linearibus, obtusis, minute apiculatis ; capitula pauciflora ; petala linearia ; stamina 10 ; legumen lineare.

Young leaves sparingly pubescent or ciliolate, the plant otherwise glabrous. Stem apparently erect, slender, the few branches short; stipules subulate, 3–4 mm. long; leaves about 6 cm. long, or shorter, the petioles short, the rachis of some of them bearing an orbicular gland 0.7–1.2 mm. broad between each pair of pinnæ; pinnæ 4–7 pairs, 1.5–3 cm. long; leaflets 12–25 pairs, linear, membranous, obtuse, minutely apiculate, 3–6 mm. long, about 0.5 mm. wide, the midvein slender, the lateral venation obscure; peduncles about 1.5 cm. long, or shorter; heads few-flowered ; calyx about 2 mm. long, its teeth ovate ; petals linear, about 4 mm. long; stamens 10, about as long as the petals; legume linear, long-tipped. 5–6 cm. long, 3–5 mm. wide.

Thicket near the coast, Playa Brava, Santa Marta, Magdalena, Colombia, November 17, 1899, *H. H. Smith 2063,* type (N Y.).

The plant is interesting as bearing legumes 3 mm. wide on some branches and 5 mm. wide on others.

25. LEPTOGLOTTIS DC. Mem. Leg. 451. 1825.

Type species: *Leptoglottis Nuttallii* DC.

KEY TO SPECIES OF LEPTOGLOTTIS

Legume about 4 mm. thick, its beak long and slender.   1. *L. leptocarpa.*
Legume 5–6 mm. thick, its beak shorter.............   2. *L. hamata.*

1. **Leptoglottis leptocarpa** (DC.) Standley, Journ. Wash. Acad. Sci. 15: 458. 1925.

Schrankia leptocarpa DC. Prodr. 2: 443. 1825.

Type locality : Santo Domingo.
Cúcuta, Norte de Santander. *Killip & Smith 20983.* French Guiana to Paraguay and Venezuela ; Panama and Costa Rica ; Martinique ; St. Vincent.   Hispaniola (according to De Candolle).

2. **Leptoglottis hamata** (H. & B.) Standley, Journ. Wash. Acad. Sci. 15: 458. 1925.

Schrankia hamata H. & B.; Willd. Sp. Pl. 4: 1042. 1806.

Type locality : Magdalena River, Colombia.
Frequent in Colombia.   Panama.

26. MIMOSA L. Sp. Pl. 516. 1753.

Type species: *Mimosa sensitiva* L.

KEY TO SPECIES OF MIMOSA

A. Petiole eglandular.
  1. Stamens as many as the corolla-lobes.
    a. Pinnæ 1 pair; leaflets large, few.
      *Leaflets 1 or 2 pairs.   (SENSITIVÆ)
        Legume 8–12 mm. broad.

Leaflets lanceolate; legume 7–8 mm. broad,
    its margins long-setose.............. 1. *M. Velloziana.*
Leaflets ovate-lanceolate; legume 10–12
    mm. broad, its margins short-setose. 2. *M. firamenensis.*
Legume 5–6 mm. broad.
    Leaflets acute or acuminate; legume 3–4
        cm. long.
        Twigs and leaves canescent............ 3. *M. albida.*
        Leaflets strigose beneath............. 4. *M. floribunda.*
    Leaflets obtuse, rounded, or acutish; legume
        about 1.5 cm. long, densely setose.
        Leaflets obovate to elliptic........... 5. *M. debilis.*
        Leaflets oblong .... 6. *M. panamensis.*
  **Leaflets 3 or 4 pairs. (CASTÆ)............ 7. *M. casta.*
  b. Pinnæ 1-several pairs; leaflets small, many.
  Herbaceous species. (PUDICÆ)
    Pinnæ 2 pairs............................ 8. *M. pudica.*
    Pinnæ 1 pair.
      Leaflets 30–50 pairs; petioles unarmed.... 9. *M. Killipii.*
      Leaflets 10–15 pairs; petioles prickly.... 10. *M. santanderensis.*
  Woody species.
    Pinnæ 1 pair. (POLYCARPÆ)............... 11. *M. polycarpa.*
    Pinnæ 3-many pairs.
      Pinnæ 3 pairs, approximate. (POLYDAC-
        TYLÆ)
        Sparingly appressed-pubescent or glab-
          rate .... 12. *M. polydactyla.*
        Densely long-pilose .... 13. *M. Andreana.*
      Pinnæ 8–15 pairs; flowers short-spicate.
        (SPICIFLORÆ)
        Densely white-pilose .... 14. *M. esmeraldæ.*
        Glabrous, or nearly so................ 15. *M. spiciflora.*
2. Stamens twice as many as the corolla-lobes.
  a. Flowers long-spicate.
    Plant lepidote-glandular. (TRIANÆ)......... 16. *M. Trianæ.*
    Plant not lepidote. (DISTACHÆ)
      Leaflets few pairs, elliptic to obovate...... 17. *M. oligacantha.*
      Leaflets many pairs, linear.
        Leaflets glabrous .... 18. *M. leiocarpa.*
        Leaflets pubescent .... 19. *M. tenuiflora.*
  b. Flowers capitate.
    Legume few-several-jointed, the joints broad.
      Herbaceous or suffrutescent species.
        Corolla many-nerved. (SOMNIANTES)..... 20. *M. somnians.*
        Corolla nerveless.
          Low, spreading or prostrate herbs.
            (PUSILLÆ) .... 21. *M. martensis.*
          Erect or decumbent, suffrutescent species.
            (FLAVESCENTES) .... 22. *M. flavescens.*
    Vines or shrubs.
      A long woody vine; legume linear-oblong.
        (INVISÆ) .... 23. *M. invisa.*
      A prostrate shrub; legume obovate, short.
        (DORMIENTES) .... 24. *M. dormiens.*
    Legume 15–20-jointed, the joints narrow.
      (PIGRÆ) .... 25. *M. pigra.*
B. Petiole glanduliferous; vines; pinnæ 2 pairs.
  (COLOMBIANÆ)
  Leaflets 1 pair; flowers capitate.................. 26. *M. colombiana.*
  Leaflets 1½–2½ pairs; flowers short-spicate...... 27. *M. Lawranceana.*

1. **Mimosa Velloziana** Mart.; Benth. Journ. Bot. Hook. 4: 361. 1841.

Type locality : Rio de Janeiro, Brazil.
Rio César, *Dauc 615.*   Brazil ; Panama.

2. **Mimosa jiramenensis** Karst. Fl. Col. 2: 59, *pl. 130.* 1862.

Mimosa Velloziana jiramenensis Benth. Trans. Linn. Soc. 30: 390. 1875.

Type locality : Rio Meta, Colombia.
Known to us only from Karsten's description and illustration.

3. **Mimosa albida** H. & B.; Willd. Sp. Pl. 4: 1030. 1806.

Type locality : South America (Coast of Peru, at Moche, according to Kunth).
Pacific Coast, Lima to Panama (according to Bentham).

This species has been given wide range in tropical America, by authors, north to Michoacan and Veracruz, but, as illustrated by a Peruvian specimen (*Cuming 1025*) and by Kunth's Mimosaceæ, *plate 1,* it may be restricted to the coastal region cited by Bentham. We have seen no specimens from Colombia.

4. **Mimosa floribunda** Willd. Sp. Pl. 4: 1031. 1806.

Mimosa strigosa Willd. 4: 1030.   1806.
Mimosa Willdenovii Poir. in Lam. Encycl. Suppl. 1: 50. 1810.

Type locality : Caracas, Venezuela.
Common in Colombia.   Venezuela.   ZARZA, applied to many species of this genus.

5. **Mimosa debilis** H. & B.; Willd. Sp. Pl. 4: 1029. 1806.

Mimosa Hostmannii Benth. Lond. Journ. Bot. 5: 84. 1846.
Mimosa notata Steud. Flora 26: 758. 1843.

Type locality : Caripe, Venezuela.
Colombia (according to Bentham).   Venezuela ; Surinam ; Brazil.

6. **Mimosa panamensis** (Benth.) Standley, Contr. U. S. Nat. Herb. 18: 104. 1916.

Mimosa debilis panamensis Benth. Trans. Linn. Soc. 30: 391. 1875.

Type locality : Panama.
Villavicencio, Meta. *Pennell 1618.*   Panama : Costa Rica.

7. **Mimosa casta** L. Sp. Pl. 518. 1753.

Type locality : India (according to Linnæus, but doubtless Brazil).
Dept. Bolívar, *Pennell 4184.*   Orocué, Boyacá, *Ariste Joseph A980.*   Villavicencio, Meta, *Nicéforo.*   Panama ; Brazil ; Trinidad to Guadeloupe.

8. **Mimosa pudica** L. Sp. Pl. 518. 1753.

Type locality : Brazil.
Common in Colombia.   Tropical America, north to Veracruz and the Bahama Islands.   Naturalized in Old World tropics.   RASTERA, DORMIDERA, applied to many species of this genus.

9. **Mimosa Killipii** Britton & Rose, sp. nov.

Suffrutescens vel herbacea, erecta, caule puberulo et laxe strigoso, remote aculeato vel inerme ; petioli inermes ; pinnæ 1-jugæ, foliolis 30–50-jugis, lineari-bus, acutis, membranaceis, supra puberulis, subtus strigosis ; pedunculi axillares et in fasciculo breve terminale, capitulis oblongis vel subglobosis ; calyx longi-ciliatus : corolla 4-lobata ; stamina 4 ; legumen lineari-oblongum, 2–3-articu-latum, glabrum, marginibus longisetosis.

Suffrutescent or herbaceous, erect, about 1.7 m. high, or lower, the slender stem puberulent and loosely strigose, distantly prickly, or unarmed.   Stipules nearly linear, long-ciliate, 5–6 mm. long ; petioles slender, puberulent and stri-gose, unarmed, 2–4 cm. long ; pinnæ 1 pair ; leaflets 30–50 pairs, linear, acute, 6–15 mm. long, membranous, puberulent above, strigose beneath, the venation

obsolete, the base obliquely truncate; peduncles axillary and in a short terminal cluster, very slender, strigose, about 15 mm. long, or shorter; heads oblong or subglobose, 6–10 mm. long, many-flowered; bractlets small, long-ciliate above; calyx long-ciliate; corolla 4-lobed, about 2 mm. long, the lobes pubescent above; stamens 4, about 8 mm. long; legume linear-oblong, 2 cm. long, or shorter, 4–5 mm. wide, 2–or–3-jointed, short-tipped, glabrous, the margins long-bristly.

Dry hillside, Río Suratá Valley, between El Jaboncillo and Suratá, Santander, Colombia, 1300 to 1800 m. altitude, January 3, 1927, *Killip & Smith 1641½*, type (N.Y.). Between Chinácota and La Esmeralda, Norte de Santander, Colombia, March 19, 1927, *Killip & Smith 20861*.

10. Mimosa santanderensis Britton & Rose, sp. nov.

Suffrutescens vel subherbacea, ramulis laxe pilosis, densissime aculeatis; petioli pilosi et aculeati; pinnæ 1-jugæ, foliolis linearibus, subacutis, glabris, appresso-ciliatis, 3–5-nerviis, costa subexcentrica; capitula axillaria et in racemo terminale, globosa, pedunculis pilosis; flores glabri; corolla 4-lobata; stamina 4.

Suffrutescent or subherbaceous, about 2.5 m. high, or lower, the slender branches loosely pilose and copiously short-prickly. Stipules lanceolate, acuminate, long-ciliate, about 3 mm. long; petioles very slender, pilose and prickly, 3–6 cm. long; pinnæ 1 pair, short-stalked; leaflets 10–15 pairs, linear, acutish, appressed-ciliate, 8–13 mm. long, about 2 mm. wide, membranous, glabrous on both sides, dark green above, pale beneath, 3–5-nerved, pinnately veined, the midvein somewhat excentric, the oblique base rounded; heads axillary and in a terminal raceme, globose, many-flowered; peduncles nearly filiform, pilose, about 13 mm. long, or shorter; flowers glabrous; calyx minute; corolla 4-lobed, 2 mm. long; stamens 4, white, 8–9 mm. long.

Damp thicket, Puerto Wilches, Santander, Colombia, at 100 m. altitude, November 28, 1926, *Killip & Smith 14798*, type (N.Y.).

11. Mimosa polycarpa Kunth, Mim. 8, *pl. 3*. 1819.

Type locality: Cajamarca, Peru.
Ocaña, *Schlim 173*. Venezuela to Brazil, Paraguay and Peru.

12. Mimosa polydactyla H. & B.; Willd. Sp. Pl. 4: 1033. 1806.

Type locality: Río Negro, near San Carlos, Venezuela.
Umbría, Putumayo, *Klug 1664*. Venezuela to French Guiana. Panama.

13. Mimosa Andreana Britton & Rose, sp. nov.

Suffrutescens vel herbacea, caule petiolis pedunculisque dense pilosis, caule remote aculeato, petiolis pedunculisque inermibus; pinnæ 3-jugæ, rachillis setoso-pilosis, foliolis 20–30-jugis, linearibus, acutis, laxe pubescentibus, marginibus appresso-setoso-ciliatis; capitula axillaria et in racemo terminale, oblonga; corolla 4-lobata; stamina 4.

Suffrutescent or herbaceous, the stem, petioles and peduncles densely pilose with long, yellowish-brown, bristly hairs, the stem distantly prickly, the petioles and peduncles unarmed. Stipules linear-lanceolate, acuminate, long-pilose; petioles rather stout, about 4 cm. long, or shorter; pinnæ 3 pairs, approximate; rachilla bristly-pilose; leaflets 20–30 pairs, linear, acute, 6–10 mm. long, about 1.5 mm. wide, loosely pubescent, the margins appressed-bristly-ciliate; heads axillary and in a terminal raceme, oblong, densely many-flowered, about 7 mm. long; peduncles slender, about 2 cm. long, or shorter; bractlets short, sparingly long-ciliate at apex; calyx minute; corolla 2 mm. long, 4-lobed, the lobes pubescent at apex; stamens 4, about 6 mm. long.

Mercuadores [Mercaderes, El Cauca?], Colombia, April 29, 1876, *E. André 2921*, type (N.Y.). La Mesa, Cundinamarca, *Triana*.

14. Mimosa esmeraldæ Britton, sp. nov.

Frutex vel arbor parva, ramulis petiolis rachideque dense pilosis et aculeis brevibus luteis reflexis armatis; pinnæ 8–12-jugæ, rachillis aculeatis, foliolis 20–30-jugis, linearibus, obtusis, glabris, ciliatis; flores 5-meri, puberuli, dense brevispicati, spicis axillaribus et in paniculo angusto terminale; stamina 5; legumen late lineare, glabrum 10–14-articulatum.

A shrub or small tree, 3–5 m. high, the twigs and the stout petioles and leaf-rachis densely pilose and armed with short reflexed yellow prickles. Petioles 1–2 cm. long; pinnæ 8–12 pairs, nearly sessile; rachillas prickly; leaflets 20–30 pairs, approximate, linear, obtuse, 4–5 mm. long, about 1 mm. wide, glabrous but ciliate, faintly 1-veined; flowers densely short-spicate, puberulent; spikes axillary and in a narrow terminal panicle, 2 cm. long, or shorter, the peduncles pilose, 8–12 mm. long; calyx minute, 5-lobed; corolla deeply 5-lobed, the lobes lanceolate, 1.5 mm. long; stamens 5, bluish pink, about 3 times as long as the corolla; legume broadly linear, glabrous, delicately reticulate-veined, 8–9 cm. long, about 13 mm. wide, 10–14-jointed, the joints wider than long, the apex rounded, the sparingly short-prickly margins separating.

Edge of woods, between Chinácota and La Esmeralda, Norte de Santander, Colombia, March 19, 1927, *Killip & Smith 20889,* type (N.Y.).

15. Mimosa spiciflora Karst. Fl. Col. 2: 61, *pl. 131.* 1862.

Schrankia glabra Benth. Lond. Journ. Bot. 5: 94. 1846.

Type locality: Near Caracas and Puerto Cabello, Venezuela.
Colombia, *Linden 1501* (type of *Schrankia glabra*). Venezuela.

16. Mimosa Trianæ Benth. Trans. Linn. Soc. 30: 412. 1875.

Type locality: Villavicencio, Colombia.
Villavicencio, *Triana 4453.*

17. Mimosa oligacantha DC. Prodr. 2: 429. 1825.

Type locality: Santa Marta, Colombia.
Santa Marta, Magdalena, *H. H. Smith 33; Schlim 942.* Aruba; Cuba. Included by authors in the Mexican *Mimosa distachya* Cav.

18. Mimosa leiocarpa DC. Prodr. 2: 429. 1825.

Type locality: Santa Marta, Colombia.
Santa Marta, Magdalena, *H. H. Smith 35, 302, 2066.* Venezuela?

19. Mimosa tenuiflora (Willd.) Poir. in Lam. Encycl. Suppl. 1: 82. 1810.

Acacia tenuiflora Willd. Sp. Pl. 4: 1088. 1806.
Mimosa cabrera Karst. Fl. Col. 2: 63, *pl. 132.* 1862.

Type locality: Caracas, Venezuela.
Colombia (according to Karsten). Venezuela; El Salvador; Oaxaca. CARBONAL.

20. Mimosa somnians H. & B.; Willd. Sp. Pl. 4: 1036. 1806.

Mimosa somniculosa H. B. K. Nov. Gen. & Sp. 6: 257. 1824.

Type locality: Tropical America (Andes of Colombia, according to Kunth, Mim. pl. 7).
Frequent at middle altitudes in Colombia. Venezuela (according to Pittier); Guiana (according to Bentham); Brazil; Bolivia; Paraguay; Panama to Oaxaca.

21. Mimosa martensis Britton & Rose, sp. nov.

Annua, humilis; ramuli pedunculi folii rachisque laxe longipilosa; pinnæ 2–3-jugæ, foliolis 10–20-jugis, lineari-oblongis, obtusis, ciliatis; flores capitati, capitulis parvis, globosis; corolla 4-lobata; stamina 8; legumen lineari-oblongum, laxe villosum, 2–3-articulatum.

Low, spreading or prostrate annual, the stem slender, widely branched, the twigs, peduncles and leaf-rachis loosely long-pilose. Stipules lanceolate, acu-

minate, several-nerved, 3–4 mm. long; petiole very slender, about 3 cm. long or shorter; pinnæ 2 or 3 pairs, distant, very short-stalked; leaflets 10–20 pairs, linear-oblong, membranous, 5–8 mm. long, rather strongly veined, obtuse, ciliate; peduncles about 2 cm. long, or shorter, loosely pilose; flowers capitate; heads small, globose, several-flowered; bractlets lanceolate, ciliate; calyx minute; corolla 4-lobed, nerveless; stamens 8, about 3 times as long as the corolla; legume linear-oblong, 1–1.7 cm. long, about 3 mm. wide, loosely villous, 2-or-3-jointed.

Near Masinga, Santa Marta, Magdalena, Colombia, November 17, 1898, *H. H. Smith 71½*, type (N.Y).

22. **Mimosa flavescens** Splitg. in Hoev. & Vries, Tijdscr, 9: 110. 1842.

Mimosa æschinominis Benth. Bot. Voy. Sulph. 89. 1844.

Type locality : Surinam.
Santa Marta, *H. H. Smith 301*. Girardot, Cundinamarca, *Rusby* & *Pennell 129*. Dept. Bolívar, *Killip* & *Smith 11141*, *14437; Heriberto 425*. Venezuela to Surinam; Costa Rica to Guerrero; Grenada; Martinique. Cierra puta.

23. **Mimosa invisa** Mart. Flora 20: Beibl. 121. 1837.

Schrankia brachycarpa Benth. Journ. Bot. Hook. 2: 130. 1840.

Type locality : Rio de Janeiro, Brazil.
Santa Marta, *H. H. Smith 101*. Medellín, *Archer 689; Toro 7½, 2484, 1290*. Espinal, *Apollinaire Marie*. Venezuela? Trinidad; Brazil; Guiana (according to Bentham) ; Bolivia ; Panama to Veracruz and Tepic ; Jamica ; Cuba ; Hispaniola.

24. **Mimosa dormiens** H. & B.; Willd. Sp. Pl. 4: 1035. 1806.

Mimosa intermedia Kunth, Mim. 16, *pl. 6*. 1819.

Type locality ; Río Apure, Venezuela.
Colombia (according to Bentham). Venezuela ; Guiana (according to Bentham) ; Brazil ; Costa Rica to Chiapas.

25. **Mimosa pigra** L. Cent. Pl. 1: 13. 1755.

Mimosa asperata L. Syst. ed. 10, 1312. 1759.
Mimosa pellita H. & B.; Willd. Sp. Pl. 1037. 1806.

Type locality : not cited.
Common in Colombia. Venezuela to French Guiana, Ecuador, Bolivia and Paraguay ; Panama to Sinaloa ; Trinidad to Guadeloupe ; Jamaica ; Cuba. Trupillo.

26. **Mimosa colombiana** Britton & Killip.

Mimosa bauhiniæfolia Karst. Fl. Col. 2: 65, *pl. 133*. 1862. Not Salisb.

Type locality : Villavicencio, Colombia.
Villavicencio, Meta, *Triana 4485; Sprague 93*. Cabuyaro, Meta, *Sprague 16*. Magdalena, *André 271, 451*. Puerto Wilches, Santander, *Killip & Smith 14918*. Endemic.

A specimen collected at Villavicencio by Brother Apollinaire Marie in December 1929 has young inflorescence and leaves much resembling those of *Mimosa colombiana*, but the legumes are oblong, rounded, and 2–2.5 cm. wide.

27. **Mimosa Lawranceana** Britton & Killip, Phytologia 1: 23. 1933.

Type locality : El Humbo region of western Boyacá, Colombia.
El Humbo, Boyacá, *Lawrance 600* (type).

Mimosa arenosa (Willd.) Poir. was recorded by Bentham from Colombia, in error for Venezuela.
Mimosa elliptica Benth. has been reported from Colombia,[7] but in later works of Bentham its distribution is limited to Brazil.

[7] Bot. Voy. Sulphur, p. 89.

27. MIMOSOPSIS Britton & Rose, N. Am. Flora 23: 174. 1928.

Type species: *Mimosa prolifica* S. Wats.

1. Mimosopsis quitensis (Benth.) Britton & Rose.

Mimosa quitensis Benth. Journ. Bot. Hook. 4: 408. 1842.

Type locality: Quito, Ecuador.
Western Cordillera, *Langlassé 85*. Rio Paez Valley, *Pittier 1341*. Coconuco, El Cauca, *Killip 6810*. Pasto, Nariño, *Triana 4451*. Susumuco (?) *André K. 413*. Ecuador. GUARANGO.

28. NEPTUNIA Lour. Fl. Coch. 653. 1790.

Type species: *Neptunia oleracea* Lour.

KEY TO SPECIES OF NEPTUNIA

Aquatic; stem floating, spongy, usually simple...... 1. *N. prostrata.*
Terrestrial; stem ascending, or spreading, usually
branched .... 2. *N. plena.*

1. Neptunia prostrata (Lam.) Baill. Bull. Soc. Linn. Paris 1: 356. 1883.

Mimosa prostrata Lam. Encycl. 1: 10. 1783.
Neptunia oleracea Lour. Fl. Coch. 654. 1790.
Mimosa lacustris H. & B. Pl. Aequin. 1: 55.

Type locality: India.
Dept. Bolívar, *Pennell 3930*. *Killip & Smith 14500, 14593*. Barranquilla, *Paul C.6*. Ecuador; Brazil; Veracruz; Jamaica; Cuba. Old World tropics.

2. Neptunia plena (L.) Benth. Journ. Bot. Hook. 4: 355. 1841.

Mimosa plena L. Sp. Pl. 519. 1753.

Type locality: Veracruz, Mexico.
Santa Marta, *H. H. Smith 298*. Dept. Bolívar, *Pennell 3951; Heriberto 289*. Dept. Atlántico, *Elias 381; Paul B.17*. Carnicerias, Tolima, *Lehmann 6110*. Curaçao, Trinidad, and Venezuela to French Guiana and Brazil; Panama; Lower California; West Indies.

29. NELTUMA Raf. Sylva Tell. 119. 1838.

Type species: *Neltuma juliflora* Raf.

1. Neltuma juliflora (Sw.) Raf. Sylva Tell. 119. 1838.

Mimosa juliflora Sw. Prodr. 85. 1788.
Prosopis juliflora DC. Prodr. 2: 447. 1825.

Type locality: Jamaica.
Frequent in northern Colombia at lower elevations. Curaçao, Aruba, Bonaire; Venezuela; West Indies. TRUPILLO, MANCA CABALLO.

30. STRYPHNODENDRON Mart. Flora 20²: Beibl. 117. 1837.

Type species: *Stryphnodendron Babatimum* Mart.

KEY TO SPECIES OF STRYPHNODENDRON

Pinnæ 15–20 pairs; leaflets villous, 6–10 mm. long. 1. *S. polyphyllum.*
Pinnæ 2–3 pairs; leaflets minutely puberulent, 10–20
mm. long .... 2. *S. colombianum.*

1. Stryphnodendron polyphyllum Mart.; Benth. in Mart. Fl. Bras. 15²:285. 1876.

Type locality: Serra de Mantequeira, Brazil
Colombia, *Mutis 5634*. Brazil.

2. Stryphnodendron (?) colombianum Britton & Killip, sp. nov.

Arbor, ramulis glabris; petiolus glandulosus; pinnæ 2-3-jugæ, foliolis 5-8-jugis, oppositis, oblique elliptis vel supremis obovatis, ad apicem rotundis vel emarginatis, minute puberulis; legumen lineare, planum, glabrum. coriaceum.

A tree, 8-10 m. high, the short, slender twigs glabrous. Petiole and leaf-rachis slender, puberulent, 5-8 cm. long. the petiole bearing a nearly flat, sessile, orbicular gland about 1 mm. in diameter; pinnæ 2 or 3 pairs, the very slender, puberulent rachillas 4-6 cm. long; leaflets 5-8 pairs, opposite, rarely membranous, obliquely elliptic, or (terminal pair) obovate, 10-20 mm. long, 6-12 mm. wide, delicately pinnately veined, with the midvein nearly central, minutely puberulent, the apex rounded or emarginate, the base narrowed or subtruncate; peduncles 3-5 cm. long; legume linear, flat, glabrous, coriaceous, reticulate-veined, 7-22 cm. long, 12-14 mm. wide, its apex rounded, its base rounded or obtuse, its stout stipe 3-5 mm. long.

Upper Río Lebrija Valley, northwest of Bucaramanga, Santander, Colombia, December 29, 1926, *Killip & Smith 16368,* type (N.Y.).

31. PIPTADENIA Benth. Journ. Bot. Hook. 4: 334. 1841.

Type species: *Piptadenia latifolia* Benth.

KEY TO SPECIES OF PIPTADENIA

Pinnæ 8-20 pairs; spikes 4-10 cm. long, or longer
 in fruit.
  Leaflets 5-10 mm. long, glabrous; petals nearly
    separate .... 1. *P. flava.*
  Leaflets 2-5 mm. long; corolla 5-lobed .... 2. *P. speciosa.*
Pinnæ only 2-4 pairs.
  Leaflets 2-3 mm. long; young spikes only 2-5 mm.
    long, panicled, glabrous................... 3. *P. uliginosa.*
  Leaflets 6-9 mm. long; spikes 4-5 cm. long,
    puberulent .... 4. *P. similis.*

1. Piptadenia flava (Spreng.) Benth. Trans. Linn. Soc. 30: 371. 1875.

Acacia flava Spreng.; DC. Prodr. 2: 469. 1825.

Type locality: Santa Marta, Colombia.
Frequent in northern Colombia. Ecuador; Venezuela; Trinidad; Panama to Colima, Mexico.

2. Piptadenia speciosa Britton & Killip, sp. nov.

Arbor parva; petiolus prope basim glandulosus; pinnæ 12-20-jugæ. foliolis 25-40-jugis, anguste linearibus, subacutis vel obtusis, sparse puberulis vel glabris, costa excentrica: flores dense spicati, glabri; corolla 5-lobata; legumen lineare, planissimum, glabrum.

Shrub or small tree, 4-6 m. high, the verrucose twigs sparingly armed with short, divaricate or ascending prickles. Leaves 10-15 cm. long, the petioles bearing a sessile oblong concave gland, the rachises and rachillas glabrous or sparingly puberulent; pinnæ 12-20 pairs; leaflets 25-40 pairs. narrowly linear, 3-5 mm. long, about 1 mm. wide, obtuse or subacute at apex, obliquely subtruncate at base. sparingly puberulent or glabrous, faintly 3-nerved, sparingly pinnate-veined, the midnerve excentric; peduncles slender, 2-6 cm. long; flowers densely spicate, glabrous, the spikes 8-10 cm. long, about 2.5 cm. thick when in full flower; calyx 1.5 mm. long, with 5 short teeth; corolla 4-5 mm. long. its 5 lobes lanceolate, acute; stamens 10, distinct, about 15 mm. long; legume linear, very flat, glabrous, strongly reticulate-veined, obtuse, apiculate, 5-13 cm. long,

10–16 mm. wide, narrowed at the base into a very slender stipe 1.5–2 cm. long, the narrow margins slightly elevated.

Barranquilla, Atlántico, Colombia, August, 1928, *Elias 513*, type (U.S), 394; *Dugand 48, 895.* Cartagena, *Heriberto 373.* Turbaco, Bolívar, *Killip & Smith 14431.* Arjona, Bolívar, *Killip & Smith 14501.* Santa Marta, *Record 26.*

3. Piptadenia (?) uliginosa Britton & Killip, sp. nov.

Frutex ubique glaber, ramis aculeis crassis recurvatis armatis, ramulis inermibus; petiolus glandulosus; pinnæ 2–4-jugæ, foliolis 6–10-jugis, lineari-oblongis, trinerviis, costa excentrica; paniculæ conicæ, 2–4 cm. longæ e racemis parvis numerosis compositæ.

A shrub, 1–3 m. high, glabrous throughout, the rather stout branches armed with stout recurved prickles about 2 mm. long, the numerous slender twigs unarmed. Stipules subulate, 1–2 mm. long; petiole and leaf-rachis nearly filiform, 2–4 mm. long; petiole bearing an orbicular or oblong-orbicular sessile concave gland about 0.5 mm. broad; pinnæ 2–5 pairs, about 2 cm. long, or shorter, the rachilla filiform; leaflets 6–10 pairs, linear-oblong, membranous, 2–3 mm. long, about 1 mm. wide, acute or obtuse, 3-nerved at base, and pinnately few-veined, the midvein excentric; inflorescence a panicle of slender racemes, 2–4 cm. long, bracteolate, the racemes 5–8 mm. long, several-flowered, on filiform peduncles; calyx about 0.5 mm. long, minutely 5-toothed; corolla 1.5 mm. long, the petals free nearly to base; stamens 10, distinct, about 3 mm. long.

In mud, Los Volcanes, near Turbaco, Bolívar, Colombia, 200–300 m. altitude, November 12, 1926, *Killip & Smith 14453*, type (N.Y.). Galapa, Atlántico, *Dugand 740.*

4. Piptadenia similis Britton & Killip, sp nov.

Ramuli et folia inermia; petiolus glandulosus; pinnæ 3–4-jugæ, foliolis 10–17-jugis, oblongis, subtus pallidis, puberulis, costa subexcentrica; spicæ dense puberulæ; corolla puberula; stamina 9; ovarium stipitatum, dense pilosum.

Twigs and leaves unarmed, the young twigs, leaf-rachis and rachillæ densely puberulent. Pinnæ 3 or 4 pairs, 5–7 cm. long; petiole about 2 cm. long, or shorter, bearing a suborbicular sessile depressed gland about 1 mm. in diameter; leaflets 10–17 pairs, oblong, chartaceous, rounded, 6–9 mm. long, 2–3 mm. wide, faintly shining and glabrous above when old, pale and puberulent beneath, the midvein slightly excentric, the lateral venation delicate; spikes few-together, slender, densely puberulent, 4–5 cm. long, many-flowered; calyx 5-toothed, about 1 mm. long, the triangular teeth acute, corolla puberulent, deeply 5-lobed, about 2 mm. long, the lanceolate lobes acute; stamens 9, about 3 mm. long; ovary densely pilose, stipitate.

Usiacuri, Barranquilla, Atlántico, Colombia, 250 m. elevation, July, 1927, *Elias 263*, type (U.S.).

Similar to *P. Pittieri* Harms, of Venezuela.

The type locality of *Piptadenia subtiliifolia* (H. B. K.) Benth., "In ripa fluminis Chotae, . . . (Regno Novo-Granatensi)," is in present-day Ecuador.

NOTE. *Goldmania foetida* (Jacq.) Standley (*Mimosa foetida* Jacq., *Inga foetida* Willd., *Acacia foetida* H. B. K., *Piptadenia foetida* Benth.) was described by Jacquin in 1798 from a cultivated plant, grown from seeds of uncertain origin. In 1824, Humboldt, Bonpland and Kunth assigned it to "Mescala and Venta de Estola, Andes of New Spain", and record (Nov. Gen. & Sp. 7: 433) these localities as in Mexico. Bentham, however (Trans. Linn. Soc. 30: 366) states, apparently in error, that Mescala is in Colombia.

32. ENTADA Adans. Fam. Pl. 2: 318. 1763.

Type species: *Mimosa Entada* L.

1. Entada gigas (L.) Fawcett & Rendle, Fl. Jam. 4²: 124. 1920.

Mimosa gigas L. Pl. Jam. 22. 1759.
Mimosa scandens L. Sp. Pl. ed. 2, 1501. 1763.
Entada scandens Benth. Journ. Bot. Hook. 4: 332. 1842.

Type locality: Jamaica.
Santa Marta, *H. H. Smith 2113.* Venezuela; Honduras; Mexico; Jamaica; Cuba; Hispaniola; Martinique; St. Vincent. Old World tropics.

33. ENTADOPSIS Britton; Britton & Rose, N. Am. Flora 23: 191. 1928.

Type species: *Mimosa polystachya* L.

1. Entadopsis polystachya (L.) Britton; Britton & Rose, N. Am. Flora 23: 191. 1928.

Mimosa polystachya L. Sp. Pl. 520. 1753.
Entada polystachya DC. Mem. Leg. 434. 1825.

Type locality: Tropical America.
Magdalena, *André 213.* Santa Marta, *H. H. Smith 878.* Lands of Loba, Bolívar, *Curran 173, 361.* French Guiana to Trinidad, Tobago and Venezuela; Ecuador; Panama to Guerrero; Grenada to Guadeloupe; Hispaniola. Bejuco de garza.

34. PARKIA R. Br. in Denham & Clapp, Narr. Trav. Africa, App. 234. 1826.

Type species: *Parkia africana* R. Br.

KEY TO SPECIES OF PARKIA

Pinnæ 5 or 6 pairs; leaflets several pairs, about 2 cm.
long .... 1. *P. arborea.*
Pinnæ 10 pairs or more; leaflets many pairs, about 12
mm. long .... 2. *P. multijuga.*

1. Parkia arborea (Karst.) Britton & Killip.

Paraphosphæra arborea Karst. Fl. Col. 2: 7, *pl. 104.* 1862.
Parkia Paraphosphæra Benth. Trans. Linn. Soc. 30: 363. 1875.

Type locality: Eastern declivity of the Cordillera of Bogotá, Colombia.
Known to us only from description and Karsten's illustration

2. Parkia multijuga Benth. in Mart. Fl. Bras. 15²: 266. 1876.

Type locality: Ega, Brazil.
Río Caquetá, Caquetá, *Ducke 12313.* Brazil.

GENERA OF CÆSALPINIACEÆ IN COLOMBIA

KEY TO GENERA

A. Calyx gamosepalous or polysepalous.
  Leaves entire, 2-lobed, or 2-parted. (BAUHINIEÆ)
    Five or more stamens antheriferous.
      Calyx tubular, the limb spathaceous......... 1. BAUHINIA.
      Calyx oblong to campanulate.
        Anther-bearing stamens 10............... 2. SCHNELLA.
        Anther-bearing stamens 9................ 3. AMARIA.
      Only 1 stamen antheriferous.................. 4. CASPAREOPSIS.
  Leaves pinnate, bipinnate, or 2-foliolate.
    1. Leaves pinnate or 2-foliolate. (See *Hæmatoxylon.*)
      a. Anthers dorsifixed versatile, longitudinally dehiscent.

Calyx gamosepalous; leaves pinnate.
  Stamens 5; staminodes 5; legume broad,
    woody, dehiscent; large trees, the
    leaflets few and large. (MOREÆ).... 5. MORA.
  Stamens 10; legume narrow, membranous,
    indehiscent; small trees, the leaflets
    many, small. (POEPPIGIEÆ)......... 6. POEPPIGIA.
Calyx polysepalous.
  Stipe of the ovary free from the calyx or
    receptacle. (CYNOMETREÆ)
    Calyx 5-parted .... 7. PRIORIA.
    Calyx 4-parted .... 8. COPAIFERA.
  Stipe of the ovary adnate to the calyx or
    receptacle. (AMHERSTIEÆ)
    Bractlets small, minute, or none.
      Petals 5.
        Leaflets only 1 pair, broad; stamens
          10.
          Stigma small: legume large, in-
            dehiscent; flowers large ... .. 9. HYMENÆA.
          Stigma discoid; legume dehis-
            cent; flowers small........... 10. PELTOGYNE.
        Leaflets many pairs, narrow; le-
          gume fleshy, indehiscent; fertile
          stamens 3 .... 11. TAMARINDUS.
      Petals only 3, or none.
        Petals 3 .... 12. HETEROSTEMON.
        Petals none .... 13. CRUDIA.
    Bractlets large, deciduous or persistent.
      Upper petal large, the others rudimen-
        tary.
        Legume flat, suborbicular, rounded;
          leaves pinnate .... 14. OUTEA.
        Legume oblong to linear.
          Legume oblong, subligneous; leaves
            2-foliolate .... 15. MACROLOBIUM.
          Legume linear, elongated; leaves
            pinnate, the numerous leaflets
            acuminate .... 16. PSEUDOVOUAPA.
      Petals large, unequal .... 17. BROWNEA.
b. Anthers basifixed, opening by terminal pores,
  or slits. (CASSIEÆ)
  Petals only 1 or 2, small, or none: large
    trees .... 18. DIALIUM.
  Petals 5.
    *Legume not elastically dehiscent.
      †Legume terete or subterete, or turgid.
        ‡Legume elongated, woody, indehis-
          cent; trees with eglandular leaves;
          perfect stamens usually 10....... 19. CASSIA.
        ‡‡Legume coriaceous or chartaceous;
          perfect stamens usually 7.
          §Legume coriaceous tardily dehis-
            cent; trees with eglandular
            leaves .... 20. PSEUDOCASSIA.
          §§Legume chartaceous; leaves glan-
            duliferous.
            Shrubs, trees, or woody vines.

Legume dehiscent along 1 suture;
leaflets 4, broad .... 21. CHAMÆFISTULA.
Legume indehiscent, or bursting
irregularly; leaflets 6. or more. 22. ADIPERA.
Herbs, with very slender dehiscent
legumes .... 23. EMELISTA.
††Legume flat or 4-winged.
Legume 4-winged; large shrub with
eglandular leaves .... 24. HERPETICA.
Legume flat; trees or shrubs.
§Legume not breaking transversely.
dehiscent.
Leaves eglandular.
Petals strongly color-veined: le-
gume thin .... 25. CHAMÆSENNA.
Petals not s t r o n g l y color-
veined; legume coriaceous... 26. SCIACASSIA.
Leaves glanduliferous.
Gland borne near the base of the
petiole .... 27. DITREMEXA.
Gland borne between the leaflets. 28. PEIRANISIA.
§§Legume coriaceous, indehiscent.
at length breaking transversely;
leaves eglandular .... 29. ISANDRINA.
**Legume elastically dehiscent; funicle
short; herbs and shrubs.
Petals unequal; leaves almost always
glanduliferous .... 30. CHAMÆCRISTA.
Petals equal or nearly so; leaves eglandu-
lar .... 31. GRIMALDIA.
2. Leaves bipinnate, except in *Hæmatoxylon*.
(CÆSALPINIEÆ)
a. Ovary free from the calyx-tube.
Leaf-rachis very short, spine-tipped; legume
torulose .... 32. PARKINSONIA.
Leaf-rachis elongated, not spine-tipped.
Calyx-segments valvate.
Legume woody, very large: unarmed tree.
with very large scarlet or orange
flowers .... 33. DELONIX.
Legume coriaceous, small; spiny trees
with small yellow flowers......... 34. CERCIDIUM.
Calyx-segments imbricated.
Legume splitting at the middle of the
valves: leaves once-pinnate...... .. 35. HÆMATOXYLON.
Legume dehiscent along the sutures or
indehiscent.
*Legume indehiscent.
Lower calyx-segment entire........ 36. LIBIDIBIA.
Lower calyx-segment lacerate or
fimbriate.
Legume coriaceous, compressed:
prickly tree or shrub .... .. 37. TARA.
Legume thin, very flat; unarmed
trees or shrubs .... 38. BRASILETTIA.
**Legume dehiscent.
Seeds flat or compressed; legume
flat, unarmed.
Stamens elongated; petals large. 39. POINCIANA.

Stamens short; petals small.. .. 40. CÆSALPINIA.
Seeds subglobose; legume com-
pressed, prickly .... 41. GUILANDINA.
b. Ovary adnate to the calyx tube; unarmed
trees .... 42. SCHIZOLOBIUM.
B. Calyx entire. closed in bud, rupturing at anthesis.
(SWARTZIEÆ)
Trees or shrubs: flowers mostly with 1 large petal
only .... 43. SWARTZIA.

1. BAUHINIA [Plum.] L. Sp. Pl. 374. 1753.

Type species: *Bauhinia aculeata* L.

KEY TO SPECIES OF BAUHINIA

1. Prickly species.
Flower-bud at anthesis 4 cm. long or longer: petals
narrowly linear .... 1. *B. Pauletia.*
Flower-bud much shorter; petals oblong to oblance-
olate, or obovate.
Leaves shallowly 2-lobed or emarginate........ 2. *B. emarginata.*
Leaves 2-lobed to about the middle........... 3. *B. Schultzei.*
2. Unarmed species.
Petals linear or nearly so. less than 8 mm. broad.
Leaf-lobes broadly rounded at apex............ 4. *B. conceptionis.*
Leaf-lobes acute or subacute.
Petals about 3 cm. long; leaves finely puberu-
lent beneath .... 5. *B. ungulata.*
Petals about 10 cm. long: leaves glabrous...... 6. *B. tarapotensis.*
Petals oblanceolate or obovate, more than 8 mm.
broad.
Leaves glabrous. the lobes deltoid. subobtuse.... 7. *B. picta.*
Leaves finely puberulent beneath, the lobes broadly
ovate, usually acuminulate or short-caudate.. 8. *B. Kalbreyeri.*

1. Bauhinia Pauletia Pers. Syn. 1: 455. 1805.

Type locality: Panama.
Dept. Bolívar. *Killip & Smith 14300; Heriberto 312, 489.* Santa Marta, *Record 20.*
Barranquilla, *Elias 769.* Trinidad; Venezuela; Panama to Sinaloa; Puerto Rico. PATA
DE VACA.

2. Bauhinia emarginata Mill. Gard. Dict. ed. 8, no. 5. 1768.

?Bauhinia rotundata Mill. Gard. Dict. ed. 8, no. 7. 1768.
Bauhinia mollicella Blake, Contr. Gray Herb. 53: 32. 1918.
Bauhinia mollifolia Pittier, Arb. & Arb. Venez. dec. 6-8: 88. 1927.
Type locality: Cartagena, Colombia.
Cartagena (type in British Museum).
Dept. Atlántico. *Elias 1202; Dugand 399.* Suratá, Santander, *Killip & Smith*
16242, 16525, 16528. Chinácota, Norte de Santander, *Killip & Smith 20886.* Venezuela.
PATA DE VACA.

3. Bauhinia Schultzei Harms, Repert. Sp. Nov. Fedde 24: 210. 1928.

Type locality: Upper Rio Frio, Colombia.
Rio Frio, Magdalena, *Schultze 428* (photograph of type); *Pittier 1718; Walker*
1263. Endemic.

4. Bauhinia conceptionis Britton & Killip, sp. nov.

Arbor inermis, ramulis inflorescentiaque minute puberulis; folia orbiculato-
reniformia, 11-nervia. emarginata, supra glabra, subtus minute puberula, lobis

rotundatis; petala fere linearia, longe unguiculata; stamina longiora petalis subæqualia; ovarium stipitatum.

A sparsely branched tree, about 9 m. high, the unarmed twigs and the inflorescence finely puberulent. Petioles slender, glabrate, about 4 cm. long; leaf-blades orbicular-reniform, nearly membranous, 11-nerved, reticulate-veined, dull, emarginate, shallowly cordate, the lobes broad, rounded, light green, and glabrous above, pale, and minutely and sparingly puberulent beneath; flowers axillary, binate; peduncle 1.5–2.5 cm. long; pedicels 1–2 cm. long; flower-bud at anthesis about 5 cm. long, pointed, densely puberulent, about 6 mm. in diameter, the lower, constricted part 10–13 mm. long, the upper, spathaceous part deciduous; petals white, nearly linear, gradually tapering to a claw, pinnately veined, about 5 cm. long, 6–7 mm. wide; longer stamens about as long as the petals; ovary slender, densely short-pubescent, long-stipitate.

Intendencia del Chocó, Colombia: La Concepción, about 75 m. altitude, April 20-May 23, 1931, *Archer 2086,* type (N.Y.).

5. Bauhinia ungulata L. Sp. Pl. 374. 1753.

Type locality: America.
Bolívar, *Pennell 3977; Killip & Smith 14543, 14428.* Barranquilla, *Elias 659.* Venezuela; Panama to Guerrero.

6. Bauhinia tarapotensis Benth. in Mart. Fl. Bras. 15²: 198. 1870.

Florencia, Caquetá, *Pérez 623.* Umbría, Putumayo, *Klug 1830.* Peru. MACHETA VAINA.

7. Bauhinia picta (H.B.K.) DC. Prodr. 2: 515. 1825.

Pauletia picta H. B. K. Nov. Gen. & Sp. 6: 316. 1824.

Type locality: Río Magdalena, at Río Opón, Colombia.
In a park, Bucaramanga, Santander, *Killip & Smith 19066.* Determined from description, and photograph of type specimen.

8. Bauhinia Kalbreyeri Harms, Repert. Sp. Nov. Fedde 19: 65. 1923.

Type locality: Murri, Antioquia, Colombia.
Antioquia: *Kalbreyer 1802* (co-type); *Toro 790; Rusby & Pennell 43.* Bucaramanga, *Killip & Smith 14978.* Río Carare, Boyacá, *Dawe 456.* El Humbo, *Lawrance 492.* Endemic. PATA DD VACA.

Bauhinia multinervia H. B. K. with type locality near Caracas. Venezuela, was recorded by Bentham as from Colombia, apparently in error.

2. SCHNELLA Raddi, Mem. Soc. Ital. Modena 18: 411. 1820.

Type species: *Schnella macrostachya* Raddi.

KEY TO SPECIES OF SCHNELLA

A. Leaves 2-lobed or emarginate.
  1. Leaves densely pubescent or velutinous beneath.
    Leaves densely long-pubescent beneath......... 1. *S. vestita.*
    Leaves finely pubescent or velvety beneath.
      Calyx-lobes filiform .... 2. *S. nigra.*
      Calyx-lobes broad .... 3. *S. Mutisii.*
  2. Leaves glabrous on both sides or sparingly pubescent beneath.
    Leaves very large. 10–15 cm. broad............ 4. *S. umbriana.*
    Leaves much smaller.
      Leaves lobed three-fourths, the lobes narrowly lanceolate .... 5. *S. stenoloba.*
      Leaves lobed about one-fourth, the lobes broad.
        Leaves 9-nerved .... 6. *S. columbiensis.*

     Leaves 11–13-nerved .... 7. *S. longipetala.*
B. Leaves 2-foliolate, or 2-lobed to the base.
    Pedicels very short............................. 8. *S. splendens.*
    Pedicels slender, about 2 cm. long.
    Filaments glabrous: leaflets ovate............ 9. *S. Stuebeliana.*
    Filaments long-villous; leaflets oblong-lanceolate. 10. *S. nitida.*

1. Schnella vestita Benth. Pl. Hartw. 171. 1845.

Bauhinia vestita Macbride, Contr. Gray Herb. 59: 22. 1919.

Type locality: Pandi, Bogotá, Colombia.
Dept. Cund·namarca, *Hartweg 962* (type); *Lehmann 2577* (cited by Micheli as *Bauhinia cumanensis* H B K.): *Triana 4410; Pérez 2056.* Natagaima, Huila, *Rusby & Pennell 1152, 1158.* Without locality, *Mutis 46¼.* Endemic.

2. Schnella nigra Britton & Killip, sp. nov.

Ramuli petiolique rufo-tomentosi; folia suborbicularia, 11-nervia, cordata, fere ad medium bilobata, lobis obtusis vel subobtusis, supra glabra costa excepta, subtus dense pubescentia: inflorescentia laxe racemosa, rufo-tomentosa; calyx subcampanulatus, lobis filiformibus: petala oblanceolata, calyce duplo longiora, villosa; legumen obovatum, villosum, demum glabrum, nitidum, nigrum.

Twigs and petioles rufo-tomentose. Petioles slender, 1–3 cm. long; leaves suborbicular, 3–5 cm. long, 3.5–5.5 cm. wide, 11-nerved, cordate at base, 2-lobed nearly to middle. glabrous above, except grayish tomentose on midnerve, densely short-hirsute beneath. especially on nerves, the lobes obtuse or subobtuse; inflorescence loosely racemose, rufo-tomentose, the pedicels 5–10 mm. long; calyx campanulate, about 6 mm. long. appressed-rufo-hirsute, the lobes filiform 3–4 mm. long: petals oblanceolate, nearly twice as long as the calyx, villous; stamens apparently 8: legumes flat, obovate, about 6 cm. long, 3 cm. wide, villous, at length glabrous, shining, black.

Colombia, 1760–1808, *Mutis 1110, ¼218,* type (U.S.). ?Vuelta, *Holton 989* (barren). Aguachica, Norte de Santander, *Schlim 270.*

3. Schnella Mutisii Britton & Killip, sp. nov.

Ramuli petioli inflorescentiaque dense brunneo-tomentosa; folia suborbicularia, 9-nervia. cordata, apice bilobata, lobis obtusis vel subacutis, supra glabra et nitida, subtus rufo-sericea et lucentia; paniculæ spiciformes, multifloræ: calycis lobi elliptico-orbiculati, puberuli, ciliati; stamina 10.

Twigs, petioles and inflorescence densely brown-tomentose. Petioles rather stout, 1.5–2 cm. long: leaves suborbicular, 4–7 cm. broad, 9-nerved, faintly coarsely reticulate-veined. rather deeply cordate at base, 2-lobed at apex, the lobes obtuse or acutish. glabrous and shining above. densely rufo-sericeous, beneath; spike-like panicles dense. many-flowered, 6–11 cm. long; calyx-lobes elliptic-orbicular, puberulent and ciliate, 5–6 mm. long; stamens 10.

Colombia, 1760–1808, *Mutis 2375,* type (U.S.).

4. Schnella umbriana Britton & Killip, sp. nov.

Ramuli rufo-puberuli: folia suborbicularia, cordulata, supra minute puberula, subtus breviter cano-sericea, 11-nervia. ad 2/3 longitudinis bilobata, lobis acuminatis: inflorescentia terminalis. racemosa; calyx campanulatus, lobis triangulato-ovatis, obtusis; petala obovata. extus villosa; stamina 10.

Twigs rufo-puberulent. Petioles terete, wiry, 3–5 cm. long, glabrescent; leaves suborbicular in general outline, up to 15 cm. long, and broad, cordulate, subcoriaceous, minutely puberulent above, short-cano-sericeous beneath, 11-nerved. bilobed about two-thirds their length, the lobes acuminate. up to 6 cm. wide, becoming inflexed toward apex; inflorescence terminal, racemose, the

racemes up to 13 cm. long, densely flowered, the rachis and calyces rufo-tomentose; pedicels 3–5 mm. long; calyx campanulate, 5–6 mm. long, about 5 mm. in diameter, the lobes triangular-ovate, obtuse: petals obovate, 1.8–2 cm. long, 8–9 mm. wide, villous without; stamens 10, 9–10 mm. long. the filaments glabrous.

Comisaría del Putumayo, Umbría, Colombia, 325 m. altitude. forest, October–November, 1930, *G. Klug 1733*, type (N.Y.). La Vanguardia, valley of the Río Guatiquia. Meta, *André 1049*, cited by Micheli as *Bauhinia Raddiana* Bong.

5. Schnella stenoloba Britton & Killip, sp. nov.

Ramuli rufo-hirsutuli, demum glabrati; folia oblonga, cordulata, chartacea, supra sparse pilosula, subtus sparse sericea, 7-nervia, ad ³⁄₄ longitudinis bilobata, lobis anguste lanceolatis; racemi terminales, pauciflori; calyx subcylindricus, appresso-rufo-hirsutus, lobis lineari-setaceis; petala anguste oblonga; stamina 10.

Twigs slender, rufo-hirsutulous, at length glabrous. Petioles slender, 1–1.5 cm. long, rufo-hirsutulous; leaves oblong in general outline, 3.5–6 cm. long, cordulate, chartaceous, scantily pilosulous above, sparingly sericeous beneath, 7-nerved, closely reticulate, bilobed about three-quarters their length, the lobes narrowly lanceolate, up to 1 cm. wide, subobtuse; racemes terminal, few-flowered, rufo-hirsute; pedicels 6–9 mm. long; calyx subcylindric, the tube about 1.5 cm. long, 8–9 mm. in diameter, strongly nerved, appressed-rufo-hirsute, the lobes linear-setaceous, 7–9 mm. long; petals narrowly oblong, about 3 cm. long, 4–5 mm. wide, acuminate; stamens 10, about 1.5 cm. long, the filaments glabrous.

Lower Magdalena River, Colombia, September 1916, *M. T. Dawe 142*, type (U.S.). Isla brava, *André 355*.

6. Schnella columbiensis (Vogel) Benth. Bot. Voy. Sulphur 89. 1844.

Bauhinia columbiensis Vogel, Linnæa 13: 313. 1839.

Type locality: Cartagena, Colombia.
Common at lower altitudes in northern Colombia. Venezuela. BRITCO DE CADENA.

(The older name *Bauhinia glabra* Jacq., type locality also Cartagena, may belong to this species.)

7. Schnella longipetala Benth. Journ. Bot. Hook. 2: 98. 1840.

Bauhinia longipetala Walp. Repert. 1: 852. 1842

Type locality: Pacaraima and Parime mountains, British Guiana. Aplachica, Río Magdalena, *Dawe 410*. British Guiana; Brazil; Bolivia.

8. Schnella splendens (H.B.K.) Benth. Journ. Bot. Hook. 2: 97. 1840.

Bauhinia splendens H.B.K. Nov. Gen. 6: 321. 1824.

Type locality: Orinoco River, Venezuela.
Colombia, 1760–1808, *Mutis 2378*. Venezuela; British Guiana; Brazil.

A leaf collected by Triana in the Chocó, 80 m. altitude. with lobes up to 22 cm. long, much larger than any other specimens seen, may be referable to this species.

9. Schnella Stuebeliana (Harms) Britton & Killip

Bauhinia Stuebeliana Harms, Repert. Sp. Nov. Fedde 19: 65. 1923.

Type locality: Between Honda and Bogotá, Colombia.
A photograph of the type (*Stuebel 87a*) seen by us.

10. Schnella nitida Britton & Killip, sp. nov.

Ramuli minute strigosi; folia alte cordata, bifoliolata, chartacea, supra glabra, subtus laxe pubescentia, segmentis oblique oblongo-lanceolatis, obtusis, 5-nerviis; racemi terminales; calyx oblongo-campanulatus, dentibus lanceolatis; petala oblanceolata, villosa, calyce fere duplo longiora; staminorum filamenta villosa.

Twigs slender, finely strigose. Petioles slender, nearly glabrous, 2.5–5 cm. long; leaves deeply cordate, 2-foliolate, broadly ovate in outline, 5–8 cm. long, chartaceous, glabrous above, shining and sparingly loosely pubescent beneath, the segments obliquely oblong-lanceolate, obtuse, 5-nerved, finely reticulate-veined; racemes terminal, few-flowered, 5–7 cm. long; pedicels slender, 1–2.5 cm. long; calyx oblong-campanulate, strongly nerved, glabrate or sparingly appressed-pubescent when young, 1.5–2 cm. long, its teeth lanceolate, 2.5 mm. long: petals oblanceolate, about 4 cm. long and 1.5 cm. wide, densely villous; stamens about 10 mm. long, the filaments villous.

Piedras, at base of Mt. Tolima, Tolima, Colombia, at 500 m. altitude, March 1, 1876, *E. André 1938*, type (N.Y.), cited by Micheli as *Bauhinia splendens* H.B.K. Piedras, 400 m. altitude, *Triana 4411*. Without locality, *Mutis 1112, 2369, 4219*. The Triana specimen at Kew bears the name *Bauhinia hymenæfolia* in Triana's hand. This name was used for a Panama species by Hemsley (Diag. Sp. Nov. 48. 1880), who gave as author Triana.

3. AMARIA Mutis; Caldas, Sem. Nuev. Gran. 2: 25. 1810.

Type species: *Amaria petiolata* Mutis.

KEY TO SPECIES OF AMARIA

Leaves petioled: flowers terminal.................... 1. *A. petiolata.*
Leaves sessile, amplexicaul; flowers axillary........ 2. *A. sessilifolia.*

1. Amaria petiolata Mutis; Caldas, Sem. Nuev. Gran. 2: 25. 1810.

Bauhinia petiolata Triana; Hook. Bot. Mag. 103: *pl. 6277.* 1877.

Type locality: Colombia.
Tocaima, Cundinamarca, 500 m. altitude, *Triana 4412*. Without locality, *Mutis 2377, 2398* (doubtless part of type material), *2549, 4146.* Endemic. MULATICO.

2. Amaria sessilifolia Mutis; Caldas, Sem. Nuev. Gran. 2: 25. 1810.

Type locality: Colombia.
Colombia, *Mutis 2724* (type at Madrid).

4. CASPAREOPSIS Britton & Rose, N. Am. Flora 23: 217. 1930.

Type species: *Bauhinia monandra* Kurz.

1. Caspareopsis monandra (Kurz) Britton & Rose, N. Am. Flora 23: 217. 1930.

Bauhinia monandra Kurz, Journ. Asiat. Soc. Bengal 42²: 73. 1873.

Type locality: Burma.
Medellín, *Toro 249.* Venezuela to French Guiana; West Indies, widely naturalized. Native of India.

5. MORA Benth. Trans. Linn. Soc. 18: 210. 1839.

Type species: *Mora excelsa* Benth.

1. Mora megistosperma (Pittier) Britton & Rose, N. Am. Flora 23: 218. 1930.

Dimorphandra megistosperma Pittier, Journ. Wash. Acad. Sci. 5: 472. 1915.
Dimorphandra oleifera Triana; Hemsl. Biol. Centr. Am. Bot. 1: 342, hyponym, 1880.
Mora oleifera Ducke, Arch. Jard. Bot. Rio Janeiro 4: 45, hyponym, 1925.

Type locality: Near Sumacaté, southern Darien, Panama.
Buenaventura, El Valle, *Triana 4420: Killip 5217, 11761.* Panama.

6. PŒPPIGIA Presl. Symb. Bot. 1: 15. 1830.

Type species: *Pœppigia procera* Presl.

1. Pœppigia procera Presl. Symb. Bot. 1: 16. 1830.

Type locality: Cuba.
Santa Marta, *H. H. Smith 261.* Without locality, *Mutis 4283, 4684.* Brazil; El Salvador to Guerrero; Cuba.

7. PRIORIA Griseb. Fl. Brit. W. Ind. 215. 1860.

Type species: *Prioria copaifera* Griseb.

1. Prioria copaifera Griseb. Fl. Brit. W. Ind. 215. 1860.

Type locality: near Bath, Jamaica.
Forest of Darien country, Colombia, *Dawe 888.* Jamaica; Panama: Nicaragua. CATIVO, TREMENTINO.

8. COPAIFERA L. Sp. Pl. ed. 2, 557. 1762.

[COPAIVA Jacq. Enum. Pl. Carib. 4, 21. 1760.]

Type species: *Copaifera officinalis* L.

1. Copaifera Canime Harms, Repert. Sp. Nov. Fedde 24: 210. 1928.

Type locality: Santa Izabel de Hungría, Santa Marta, Colombia.
Santa Izabel de Hungría, *Schultze 608* (fragment and photograph of type). CANIME.

9. HYMENÆA L. Sp. Pl. 1192. 1753.

Type species: *Hymenæa Courbaril* L.

1. Hymenæa Courbaril L. Sp. Pl. 1192. 1753.

Type locality: Brazil.
Santa Marta, *H. H. Smith 2027.* Venezuela to French Guiana; Bolivia and Brazil; Panama to Tepic; West Indies. ALGARRABO.

10. PELTOGYNE Vogel, Linnæa 11: 410. 1837.

Type species: *Peltogyne discolor* Vogel.

1. Peltogyne pubescens Benth. Journ. Bot. Hook. 2: 96. 1840.

Type locality: British Guiana.
Magdalena Valley, *Dawe 495.* Without locality, *Mutis 2347, ?376, 3808, 4025.* Venezuela; British Guiana.

11. TAMARINDUS L. Sp. Pl. 34. 1753.

Type species: *Tamarindus indica* L.

1. Tamarindus indica L. Sp. Pl. 34. 1753.

Type locality: India.
Frequent in Colombia, naturalized after planting, as nearly throughout tropical and subtropical America. TAMARINDO.

12. HETEROSTEMON Desf. Mem. Mus. Paris 4: 241. 1818.

Type species: *Heterostemon mimosoides* Desf.

1. Heterostemon Vageleri Harms. Notizbl. 9: 291. 1925.

Type locality: Buena Fortuna, Carare, Colombia.

Known to us only from a fragment and photograph of the type specimen (*Vageler 70*).

13. CRUDIA Schreb. Gen. 282. 1789.

[APALATOA Aubl. Pl. Guian. 1: 382. 1775.]

Type species: *Crudia spicata* Willd.

1 Crudia æqualis Ducke, Arch. Jard. Bot. Rio Janeiro 3: 91. 1922.

Type locality: Río Tapajoz, near Cachoeira do Mangibal, Brazil.
Sabanagrande and Arroyo León, Atlántico, *Dugand 289, 340.* Brazil.

14. OUTEA Aubl. Pl. Guian. 1: 28, *pl. 9.* 1775.

Type species: *Outea guianensis* Aubl.

1. Outea (?) colombiana Britton & Killip, sp. nov.

Folia inflorescentiaque glabra ; foliola 3–4–juga, oblonga vel oblongo-lanceo-lata, sessilia, acuta, basi angustata ; racemi axillares, tenuissimi ; sepala oblonga vel lanceolata : ovarium longepilosum.

Foliage and inflorescence glabrous, the twigs slender. Petiole and rachis channeled and margined above ; leaflets 3 or 4 pairs, oblong to oblong-lanceolate, sessile, subchartaceous, nearly equilateral, acute, the base narrowed, the pinnate venation delicate, the midvein elevated beneath : racemes axillary, very slender, few-several-flowered, 6–9 cm. long ; pedicels very slender, 4 or 5 mm. long ; sepals oblong to lanceolate, 4–6 mm. long ; ovary slender, long-pilose.

Isthmus of San Pablo, El Chocó, Colombia, at 70 m. elevation, *Triana 4419,* type (N.Y.).

15. MACROLOBIUM Schreb. Gen. 30. 1789.

[VOUAPA Aubl. Pl. Guian. 1: 25, *pl. 7.* 1775]

Type species: *Macrolobium Vuapa* Gmel.

1. Macrolobium floridum Karst. Fl. Colomb. 1: 151, *pl. 75.* 1861.

Vuapa florida Kuntze, Rev. Gen. Pl. 1: 213. 1891.

Type locality: Puerto Cabello, Venezuela.
Quibdó, El Chocó, *Archer 2020, 2023.* Córdoba, El Valle, *Killip 11852.* Venezuela.

16. PSEUDOVOUAPA Britton & Killip, gen. nov.

Arbor inermis ; stipulæ magnæ, falcatæ ; folia bipinnata, foliolis numerosis, magnis, lanceolatis ; flores breviracemosi, receptaculo tenue, elongato, bracteolis 2, in involucrum magnum parte connatis ; sepala 4 ; petalum 1, oblongum ; stamina 3, filamentis infra villosis ; ovarii stipes ad receptaculum adnatus ; stylus fili-formis, stigmate minuto ; legumen lineare, planum, brevistipitatum, elongatum.

An unarmed tree, with bipinnate leaves, the numerous large leaflets lanceo-late, long-acuminate, the large persistent stipules falcate, the flowers in short racemes. Receptacle slender, elongated. Bractlets 2, partly united into a large involucre. Sepals 4, little longer than the receptacle. Petal 1, oblong. Stamens 3, the filaments villous below. Stipe of the ovary adnate to the receptacle ; style filiform, long ; stigma minute. Legume linear, flat, glabrous, short-stipitate, much longer than wide.

Type species: *Macrolobium stenosiphon* Harms.

1. Pseudovouapa stenosiphon (Harms) Britton & Killip.

Macrolobium stenosiphon Harms, Repert. Sp. Nov. Fedde 3: 51. 1906.

Type locality: Timbiquí and Macay rivers, Colombia.
Timbiquí, Micay, Naya, El Canca, *Lehmann 8987* (co-type). Novita, El Chocó, *Triana 4418.* Río Tutunendo, El Chocó, *Archer 2196.* La Concepción, El Chocó, *Archer 1984.* Endemic. DORMILÓN.

17. BROWNEA Jacq. Enum. Pl. Carib. 6. 1760.

Type species: *Brownea coccinea* Jacq.

KEY TO SPECIES OF BROWNEA

A. Leaves 1–4-jugate.
  Leaf rachis and petiolules pubescent, the rachis
    stout.
    Stamens united below into a tube about 1 cm.
      long; leaflets with a gland at base........ 1. *B. macrophylla.*
    Stamens free nearly to base; leaflets eglandular. 2. *B. Holtonii.*
  Leaf rachis and petiolules glabrous, the rachis
    slender.
    Inflorescence pendulous, borne on the older
      branchlets, the common peduncle more than
      7 cm. long .... 3. *B. bolivarensis.*
    Inflorescence erect or suberect, borne on the young
      branchlets, the common peduncle not more
      than 1 cm. long.
      Pedicels very slender, more than 20 mm. long,
        glabrous; leaflets 2–4 cm. wide........ 4. *B. longipedicellata.*
      Pedicels stout, 5–15 mm. long, pubescent.
        Floral sheath subequal to calyx tube; heads
          not more than 10-flowered............. 5. *B. aroinsis.*
        Floral sheath much longer than calyx tube;
          heads more than 10-flowered.......... 6. *B. Rosa-de-monte.*
B. Leaves (except uppermost) more than 4-jugate.
  Heads of flowers large, in full flower more than 10
    cm. wide; petals more than 1 cm. wide........ 7. *B. Ariza.*
  Heads of flowers smaller, less than 10 cm. wide;
    petals not more than 1 cm. wide.
    Leaflets 9–13 to a side, cordate or cordulate,
      glabrous, glaucous beneath, the rachis
      quadrangular .... 8. *B. multijuga.*
    Leaflets 6–8 to a side, acute or rarely rounded at
      base, green and minutely puberulent be-
      neath, the rachis terete.................. 9. *B. stenantha.*

1. **Brownea macrophylla** Linden, Cat. no. 18, 11. 1863; Gard. Chron. 1873: 777, *f. 149.* 1873.

Brownea antioquiensis Linden, Cat. 3. 1869.

Type locality: Antioquia, Colombia.
Mutis 964, 2953. Medellín, *Toro 107.* Mompos Island, Bolívar, *Curran 247.* El Humbo, Boyacá, *Lawrance 587, 587a.* Panama. ARIZA.

2. Brownea Holtonii Britton & Killip. sp. nov.

Arbor, ramulis petiolis rachidibusque tomentosis; folia 2–3-juga, foliolis oppositis, abrupte caudato-acuminatis, eglandulosis, subcoriaceis, supra glabris, subtus minute puberulis, eglandulosis, infimis oblongis vel ovato-oblongis. ceteris oblanceolatis: vaginæ tubuloso-campanulatæ, tomentosæ; sepala 4, ad basim conjuncta; petala 5, obovata, longe unguiculata; stamina fere ad basim libera.

A tree, the branchlets tomentose. Leaves 2 or 3-jugate. the rachis and petiole up to 12 cm. long, stout. angulate. tomentose. the leaflets opposite. with short stout petiolules 2–6 mm. long. subcoriaceous. glabrous above, beneath minutely puberulent, pilosulous on the midnerve, abruptly caudate-acuminate, eglandular, the lowest pair oblong or ovate-oblong, up to 10 cm. long and 5 cm. wide, the others oblanceolate, up to 14 cm. long and 6 cm. wide: bracts spatulate, about 4 cm. long, 2 cm. wide, short-pubescent; pedicels 6–8 mm. long. tomentose;

sheaths tubular-campanulate, 2.5–3 cm. long, 2-lipped, tomentose; sepals 4, united at base, about 4 cm. long, the anterior one 10–11 mm. wide, the others about half as wide; petals 5, obovate, up to 7 cm. long, tapering to a long claw; stamens about 6 cm. long, united only at base; ovary long-stipitate, densely tomentose.

Honda, Department of Tolima, Colombia, April 26, 1834, *I. F. Holton,* type (N.Y.).

3. **Brownea bolivarensis** Pittier, Contr. U. S. Nat. Herb. 20: 111. 1918.

Type locality: Between Norosí and Tiquisio, Department of Bolívar, Colombia. Bolívar, *Curran 142* (type).

4. **Brownea longipedicellata** Huber, Bol. Mus. Goeldi 7: 293. 1913.

Type locality: Río Caquetá, Colombia. Cupati, Caquetá, *Ducke 12353* (co-type), *10927.*

5. **Brownea aroënsis** Pittier, Contr. U. S. Nat. Herb. 18: 152. 1916.

Type locality: Aroa River, Lara, Venezuela. La Esmeralda, Norte de Santander, *Killip & Smith 20987.* Venezuela.

6. **Brownea Rosa-de-monte** Berg, Phil. Trans. Roy. Soc. London 63: 174, *pl. 8, 9.* 1773.

Type locality: Porto Bello, Panama. *Mutis 961, ╪╪32. Triana ╪╪22.* Buenaventura, El Valle, *Triana 4423.* Río Nercua, *Schott 3.* Panama. St. Vincent? Tobago?

7. **Brownea Ariza** Benth. Pl. Hartweg. 171. 1845.

Type locality: Guaduas, "Prov. Bogota," Colombia. Frequent in Colombia. ARIZA, PALO DE CRUZ, FLOR DE LA CRUZ, PALO DE ROSA.

8. **Brownea multijuga** Britton & Killip, sp. nov.

Arbor, ramulis glabris; folia 9–13-juga, rachide quadrangualata, foliolis oppositis vel suboppositis, anguste oblongo-lanceolatis. caudato-acuminatis, cordatis vel cordulatis, glabris; inflorescentia terminalis, densiflora; bracteae late ovatae; vaginae tubulosae, bilabiatae; sepala 4, anteriore aliis subduplo latiora; petala obovato-spathulata, longe unguiculata.

A tree 12 to 15 meters high, the branchlets glabrous except at the ends. Leaves 9–13-jugate, the uppermost and lowermost leaflets opposite, the others subopposite; petiole terete, stout, about 1 cm. long, appressed-rufo-hirsute; rachis 20–35 cm. long, quadrangular, glabrous, the petiolules 3–4 mm. long, rugulose, glabrous, black; leaflets narrowly oblong-lanceolate, 8–14 cm. long, 2–3.5 cm. wide (lower leaflets cordate, up to 5 cm. long, 2 cm. wide), caudate-acuminate at apex, cordulate at base, coriaceous, glabrous, glaucous beneath; inflorescence bright red, terminal, solitary, sessile, 8–9 cm. wide, densely flowered; bracts broadly ovate. 1–1.5 cm. long, minutely rufo-tomentose without; pedicels about 5 mm. long, rufo-hirsute; sheaths tubular, about 2.5 cm. long, bilabiate, hirtellous; sepals 4, about 1.5 cm. long, the anterior one about twice as broad as the others; petals obovate-spatulate, 2–2.5 cm. long, 8–10 mm. wide, long-clawed; stamens as long as the petals, the anthers oblong; pistil about 4 cm. long, the ovary densely sericeo-hirsute, the style glabrous.

Headwaters of Río Tutunendo, east of Quibdó. Intendencia del Chocó, Colombia, May 20, 21, 1931, *Archer 2177,* type (U.S.). CLAVELLÍN.

9. **Brownea stenantha** Britton & Killip, sp. nov.

Arbor, ramulis glabris; folia 6–8-juga, rachide terete, foliolis ovatis vel ovato-oblongis, caudato-acuminatis, basi acutis vel rotundatis. supra glabris, subtus minute puberulis; inflorescentia terminalis et axillaris, densiflora; bracteae late ovatae; vaginae anguste tubulosae, appresso-hirsutae; sepala 4; petala 5, obovata; stamina 11, ad 1/3 longitudinis connata.

A tree; branchlets verrucose, glabrous, subterete, the younger portion 4-sulcate. Leaves 6–8-jugate, the terminal and basal pairs of leaflets opposite, the others sometimes subopposite; petioles stout, verrucose, about 5 mm. long; rachis 20–30 cm. long, terete, glabrous or sparsely puberulent; petiolules slender, about 5 mm. long, glabrous; leaflets ovate or ovate-oblong, 5–11 cm. long, 2–4.5 cm. wide, caudate-acuminate at apex, acute or rarely rounded at base, sub-coriaceous, glabrous above, minutely puberulent beneath; inflorescence terminal and axillary, up to 9 cm. wide, densely flowered: bracts broadly ovate, about 1.5 cm. long and 2 cm. wide, rufo-tomentellous without: pedicels slender, 5–10 mm. long, hirsutulous; sheaths narrowly tubular, about 1.5 cm. long, 3 mm. wide at throat, bilabiate, appressed-hirsute: calyx tube about 2 cm. long, 0.8 mm. in diameter in lower half, 3–4 mm. wide at throat, the sepals 4, the anterior one about 4 mm. wide. the others about 2 mm. wide; petals 5, 2 cm. long, 5 mm. wide, obovate, the claw very slender; stamens 11. 3 cm. long, connate for about 1 cm., the anthers ovate, 1.5 mm. long; ovary flavo-hirsute.

Morrocoquiel, Río Sinú, Bolívar, Colombia, March 11, 1918, *Pennell 4698*, type (U.S.).

18. DIALIUM L. Mant. 1: 1. 1767.

Type species: *Dialium indum* L.

1. Dialium guianense (Aubl.) Steud. Nom. ed. 2, 1: 497. 1840.

Arouna guianensis Aubl. Pl. Guian. 1: 16, *pl. 5.* 1775.
Aruna divaricata Willd. Sp. Pl. 1: 49. 1797.
Dialium divaricatum Vahl, Enum. 1: 302. 1804.

Type locality: French Guiana.
Lands of Loba, Bolívar, *Curran 60.* Venezuela to French Guiana and Brazil; Panama to Guatemala. GRANADILLO.

19. CASSIA [Tourn.] L. Sp. Pl. 376. 1753.

Type species: *Cassia Fistula* L.

KEY TO SPECIES OF CASSIA

Sepals canescent; legume transversely rugose....... 1. *C. grandis.*
Sepals glabrous or puberulent; legume smooth...... 2. *C. moschata.*

1. Cassia grandis L. f. Suppl. 230. 1781.

Cassia brasiliana Lam. Encycl. 1: 649. 1785.

Type locality: Surinam.
Santa Marta, *H. H. Smith 2061.* Barranquilla, *Elias 696, 1204.* Lands of Loba, Atlántico, *Curran 155.* Cienaga de Oro, Bolívar, *Pennell 4127.* Medellín, *Toro 252.* Tuluá, El Valle, *Lehmann 4614.* La Paila, El Valle, *Holton 981.* Naranjo, El Valle, *André 2562* (cited by Micheli as *Cassia leiandra* Benth.). Surinam to Trinidad, Tobago and Venezuela; Greater Antilles; Panama to Guerrero. CAÑAFISTULA GRUESA, CAÑADONGA.

2. Cassia moschata H. B. K. Nov. Gen. & Sp. 6: 338. 1824.

Type locality: Mompos, Magdalena River, Colombia.
Sahagún, Bolívar, *Pennell 4082.* Mompos, *Humboldt & Bonpland* (type, Paris). British Guiana and Venezuela; Trinidad; Panama and Costa Rica.

Cassia racemosa Mill. Gard. Dict. ed. 8, no. 19. 1768. The type locality of this species is Cartagena, Colombia. Miller's description is insufficient to enable us to associate with it any specimens seen by us from Colombia.

20. PSEUDOCASSIA Britton & Rose, N. Am. Flora 23: 230. 1930.

Type species: *Cassia spectabilis* DC.

1. Pseudocassia spectabilis (DC.) Britton & Rose, N. Am. Flora 23: 230. 1930.

Cassia spectabilis DC. Cat. Hort. Monsp. 90. 1813.
Cassia speciosa H. B. K. Nov. Gen. & Sp. 6: 338. 1824. Not Schrad.
Cassia Humboldtiana DC. Prodr. 2: 489. 1825.

Type locality· Caracas, Venezuela
Frequent in Colombia. Tobago; Trinidad; Venezuela; Panama to Tabasco; Jamaica; Cuba; Hispaniola.   CASAFISTULA MACHO.

21. CHAMÆFISTULA G. Don, Gen. Syst. 2: 451. 1832.

Type species: *Cassia bacillaris* L. f.

KEY TO SPECIES OF CHAMÆFISTULA

Bracts large, lanceolate, persistent. (UNDULATÆ)... 1. *C. undulata.*
Bracts small. ovate to linear. mostly caducous.
  Sepals strongly elevated parallel-veined and reticulated. (MACROPHYLLÆ)
    Shrubs or trees; petals much longer than the sepals; leaflets glabrate, or short-pubescent beneath.
      Leaflets about 18 cm. long or shorter; petals about 10 mm. long...................... 2. *C. macrophylla.*
      Leaflets up to 32 cm. long; petals about 2 cm. long .... 3. *C. gigantifolia.*
    A tall herb; leaflets pilose beneath; petals little longer than the longer sepals.............. 4. *C. Hazenii.*
  Sepals veinless or delicately parallel-veined.
    A. Leaflets acuminate.
      Flowers large; petals 15–25 mm. long; sepals delicately parallel-veined. (SMITHIANÆ)
        Leaflets membranous; pedicels filiform; sepals orbicular to elliptic........... 5. *C. Smithiana.*
        Leaflets chartaceous; pedicels slender; sepals oblong to ovate.
          Leaflets few-veined, gradually acuminate. 6. *C. huilana.*
          Leaflets several-veined. abruptly acuminate. 7. *C. fluviatilis.*
      Flowers relatively small; petals 10–12 mm. long. (CURRANLÆ)
        1. Leaflets definitely inequilateral.
          a. Leaflets membranous or subchartaceous.
            Inflorescence a terminal elongated panicle .... 8. *C. angusta.*
            Inflorescence axillary, few-flowered, very short .... 9. *C. Klugii.*
          b. Leaflets thick-chartaceous .... 10. *C. acuminata.*
        2. Leaflets scarcely inequilateral.
          Upper leaflets about 7 cm. long; young legume constricted between the seeds. 11. *C. tocotana.*
          Upper leaflets 9–16 cm. long.
            Leaflets abruptly acuminate; pedicels long .... 12. *C. Curranii.*
            Leaflets gradually acuminate; pedicels short .... 13. *C. oxyphylla.*

B. Leaflets acute or obtuse.
  1. Twigs inflorescence, and under leaf-sur-
    faces densely rufo-villous; flowers about
    5 cm. broad. (SPECIOSÆ) .... 14. *C. speciosa.*
  2. Plants glabrous or sparingly pubescent;
    flowers much smaller. (BACILLARES)
    Leaflets subcoriaceous, 4–8 cm. long........ 15. *C. subcoriacea.*
    Leaflets chartaceous or membranous. longer.
      a. Leaflets elliptic, very obtuse, apiculate. 16. *C. apiculata.*
      b. Leaflets ovate to obovate, not apiculate.
      Leaflets membranous, slightly inequi-
        lateral .... 17. *C. Toroana.*
      Leaflets chartaceous, definitely inequi-
        lateral.
        Twigs and inflorescence glabrous.
        Petals 20–25 mm. long............. 18. *C. inæquilatera.*
        Petals only 10 mm. long; legume
          delicately reticulate-veined .... 19. *C. tolimensis.*
        Twigs and inflorescence puberulent.
        Petals about 10 mm. long; foliage
          pale green; legume very slender,
          puberulent .... 20. *C. bolivarensis.*
        Petals 20–25 mm. long; foliage dark
          green .... 21. *C. bacillaris.*
Inflorescence unknown: rachis gland very small,
  globose; leaflets ovate; legume 20 cm. long.
  (MICRADENLÆ) .... 22. *C. micradenia.*

1. **Chamæfistula undulata** (Benth.) Pittier, Trab. Mus. Com. Venez. 3: 151.
   1928; Arb. & Arb. Legum. 121. 1928.

  Cassia undulata Benth. Journ. Bot. Hook. 2: 76. 1840.

Type locality: British Guiana.
Malena, Antioquia, *Pennell 3774.* Sahagún, Bolívar, *Pennell 4102.* Chinácota,
Norte de Santander, *Killip & Smith 20850.* Medellín, *Toro 1021* Popune. *Allen 857.*
Honda, Tolima, *André 697 bis,* cited by Micheli as *Cassia quinquangulata.* Venezuela;
Trinidad; British Guiana; Panama to Yucatán.

2. **Chamæfistula macrophylla** (Kunth) G. Don, Gen. Syst. 2: 451. 1832.

  Cassia macrophylla Kunth, Mim. 126, *pl. 38.* 1819.

Type locality: Near Cartagena, Colombia.
Frequent in Colombia. Endemic.

3. **Chamæfistula gigantifolia** Britton & Killip, sp. nov.

    Frutex vel arbor, ramis glabris: folia maxima, rachide inter jugum in-
ferius foliolorum glandulosa, glandula oblonga, foliolis chartaceis, glabris,
acuminatis, ellipticis vel elliptico-lanceolatis; inflorescentia subcorymbosa,
sparse puberula; sepala oblonga vel elliptica, reticulata; petala oblonga vel
elliptica.

    A shrub, or a tree up to about 4 m. high, perhaps higher. the stout branches
glabrous. Leaves very large, the glabrous rachis up to 22 cm. long, bearing an
oblong gland between the lower pair of leaflets; leaflets chartaceous, glabrous,
pinnately many-veined and finely reticulated. acuminate, dull, slightly in-
equilateral, elliptic or elliptic-lanceolate, the upper pair up to 35 cm. long and
15 cm. wide, the lower pair somewhat smaller; inflorescence subcorymbose,
sparingly puberulent, borne. at least sometimes. on the main stem: peduncle
2–3 cm. long; pedicels very slender, 3–4 cm. long; sepals oblong to elliptic, ob-

tuse, elevated-veined and reticulated, about 10 mm. long; petals oblong to elliptic, clawed, 16–20 mm. long.

In forest, Río Putumayo, Peru-Colombia boundary, September 26, 1930, *G. Klug 1622*, type (N.Y.). Mishuyacu, Loreto, Peru, *G. Klug 279*.

4. Chamæfistula Hazenii Britton & Killip, sp. nov.

Herba alta, ramis foliorum rachidibus brevipubescentibus; rachis inter jugum inferius foliolorum glandulosa, glandula oblongo-conica; foliola subchartacea, acuta vel subacuminata, supra glabra, subtus pilosa, subæquilateralia, superiora elliptica, inferiora ovata; inflorescentia axillaris; sepala elliptico-obovata, valde parallelo-venia et reticulata; petala obovata vel oblonga.

A tall herb, with stout short-pubescent branches and leaf-rachis. Rachis 10–12 cm. long, bearing an oblong-conic gland between the lower pair of leaflets; leaflets subchartaceous, acute or short-acuminate, distinctly pinnately veined and very finely reticulated, dull, glabrous above, pilose beneath, nearly equilateral, 9–18 cm. long, the lower pair ovate, the upper nearly elliptic; inflorescence axillary, several many-flowered; peduncle 2–3 cm. long; pedicels slender, 3.5 cm. long, or shorter; sepals elliptic-obovate, rounded, strongly parallel-veined and reticulated, 9–12 mm. long; petals obovate to oblong, 10–15 mm. long.

In forest, La Palmita, west of Armenia, Caldas, Colombia, 1100–1300 m. altitude, July 23, 922, *Pennell, Killip & Hazen 8613*, type (U.S.).

5. Chamæfistula Smithiana Britton & Rose, sp. nov.

Frutex, ramulis glabris; folia glabrata, rachide inter jugum inferius glandulosa, glandula oblonga, foliolis ovatis vel ovato-lanceolatis, acuminatis vel acutis, membranaceis; inflorescentia subpaniculata, pedicellis filiformibus; sepala orbiculata vel elliptica, tenuiter venosa.

A shrub, 2–3 m. high, with very slender, glabrous twigs. Stipules linear-lanceolate, 8–12 mm. long, deciduous; leaves glabrous, or sparingly pubescent when young; petioles 2–3 cm. long; rachis bearing an oblong gland between the lower pair of leaflets; leaflets ovate or ovate-lanceolate, acuminate or acute, 4–10 cm. long, membranous, glabrous; inflorescence subpaniculate; pedicels filiform, 2.5 cm. long, or shorter, sparingly pubescent; sepals orbicular to elliptic, glabrous, delicately parallel-veined, rounded, about 6 mm. long; petals 15–25 mm. long, glabrous.

Santa Marta, Colombia. Type from five miles east of Cienega, September 10, 1898, *H. H. Smith 251*, type (N.Y.), *250*.

6. Chamæfistula huilana Britton & Rose, sp. nov.

Frutex scandens, ramis foliisque glabris; rachidis glandula inter jugum inferius foliolorum; foliola chartacea, sensim acuminata, inferiora ovata, superiora lanceolata vel oblongo-lanceolata; panicula terminalis, pedicellis tenuissimis; sepala oblonga, tenuiter venosa.

A vine-like shrub, the leaves and slender branches glabrous. Petioles stout, about 4 cm. long, or shorter; gland borne between the lower pair of leaflets; leaflets chartaceous, gradually acuminate, the lower pair ovate, 6–9 cm. long, the upper pair lanceolate or oblong-lanceolate, 9–13 cm. long; inflorescence a terminal panicle, its branches glabrous, or finely puberulent above; pedicels very slender, 2–4 cm. long; sepals oblong, puberulent or glabrate, delicately parallel-veined, 6–10 mm. long; petals 15–20 mm. long.

Cordillera Oriental, east of Neiva, Huila, Colombia, 2000–2500 m. altitude, forest, August 1–8, 1917, *Rusby & Pennell 639*, type (N.Y.), *856*.

7. Chamæfistula fluviatilis Britton & Killip, sp. nov.

Frutex ramosissimus, ramulis flexilibus inflorescentia foliorum rachideque puberulis; rachidis glandula oblonga, inter jugum inferius foliolorum; foliola

subchartacea, valde inæquilateralia, abrupte breviter acuminata, dense reticulata, supra glabra, subtus laxe et breviter pubescentia, inferiora ovata, superiora anguste obovata; flores pauci, laxe fasciculati, pedicellis tenuibus; sepala ovata, tenuiter venosa; petala oblonga, pubescentia.

A much-branched shrub, 2–3 m. high, the slender zigzag twigs, the inflorescence, and leaf-rachis puberulent. Rachis 3–5 cm. long, bearing an oblong gland between the lower pair of leaflets; leaflets subchartaceous, definitely inequilateral, rather abruptly short-acuminate, rather closely pinnately 10–13-veined and closely reticulated, glabrous above, loosely short-pubescent beneath, the lower pair ovate, 5–7 cm. long, the upper narrowly obovate, 6–10 cm. long; flowers few, loosely clustered; pedicels slender, about 3 cm. long; sepals ovate, obtuse, glabrate, delicately parallel-veined, 5–6 mm. long; petals oblong, obtuse, pubescent, about 15 mm. long; young legume very slender, sparingly appressed-pubescent, about 15 cm. long, 2 mm. thick.

In thickets along river, vicinity of Puerto Wilches, Santander, Colombia, 100 m. altitude, November 28, 1926, *Killip & Smith 14782*, type (N.Y.). Río de Oro, Norte de Santander, *Kalbreyer 696*.

8. Chamæfistula angusta Britton & Killip, sp. nov.

Arbor parva, ramulis tenuissimis, sparse pubescentibus; glandula linearis, acuta, inter jugum inferius foliolorum; foliola membranacea, glabra, obliqua, acuminata, inæquilateralia, superiora late oblanceolata, inferiora ovata; panicula angusta, elongata, terminalis, pubescens; sepala rotundata vel obtusa.

A low tree, with very slender, sparingly pubescent twigs. Petioles slender, pubescent, about 2.5 cm. long, or shorter; gland linear, pointed, about 2 mm. long, borne between the lower pair of leaflets; leaflets thin, glabrous, oblique, acuminate, narrowed at the base, inequilateral, the upper pair broadly oblanceolate, 9–12 cm. long, about 4 cm. wide, the lower pair ovate, 5–7 cm. long; flowers numerous in a narrow terminal panicle, its axis and the pedicels pubescent; pedicels 6–12 mm. long; sepals rounded or obtuse, 3–5 mm. long; petals puberulent, about 1 cm. long; anthers about 6 mm. long.

Thickets near Río Guatiquia, Villavicencio, Meta, Colombia, 500 m. altitude, Sept. 1, 2, 1917, *Pennell 1585* type (N.Y.).

9. Chamæfistula Klugii Britton & Killip, sp. nov.

Scadens, ramis rachideque sparse et breviter pubescentibus; glandula inter juga ambo foliolorum; foliola subchartacea, glabra, acuminata, inæquilateralia, laxe reticulata, inferiora ovata, superiora late lanceolata; inflorescentia brevis, axillaris, pauciflora, dense puberula; sepala oblongo-elliptica; petala obovata.

Liana, the branches and leaf-rachis sparingly short-pubescent. Rachis slender, bearing a slender gland between both pairs of leaflets; leaflets subchartaceous, glabrous, acuminate, inequilateral, pinnately several-veined and loosely reticulated, the lower pair ovate, about 6 cm. long, the upper broadly lanceolate, 10–13 cm. long; inflorescence short, axillary, few-flowered, rather densely puberulent; peduncle only about 2 cm. long; pedicels about 15 mm. long, or shorter; sepals densely puberulent, oblong-elliptic, obtuse, 8–9 mm. long; petals obovate, 10–11 mm. long.

In forest, Comisario del Putumayo, Umbria, Colombia, 325 m. altitude, November 11, 1930, *G. Klug 1751*, type (N.Y.). Without definite locality, *Mutis 2441*.

10. Chamæfistula acuminata Britton & Killip, sp. nov.

Folia glabra, foliolis crasso-chartaceis, acuminatis, dense reticulatis, superioribus oblongo-lanceolatis, inferioribus ovatis; flores subracemosi, pedicellis strigosis; sepala oblonga, glabra; petala pubescentia; legumen glabrum, breviter acutum.

Foliage glabrous. Petioles 2–2.5 cm. long; leaflets rather thick-chartaceous, finely reticulate-veined, sharply acuminate, the lower pair ovate, 3–6 cm. long,

the upper pair oblong-lanceolate or oblong-oblanceolate, 5–9 cm. long; flowers subracemose; pedicels slender, strigose, about 1.5 cm. long; sepals oblong, obtuse or rounded, glabrous, about 4 mm. long; petals pubescent, 10–12 mm. long; legume glabrous, short-tipped, 22 cm. long, about 1.5 cm. thick.

Independence Park, Medellín, Colombia, March, 1927, *Toro 61*, type (N.Y.).

11. Chamæfistula tocotana Rose, sp. nov.

Arbor parva, fere ubique glabra: foliola oblongo-lanceolata, acuminata, glandula inter jugum inferius; inflorescentia axillaris; petala oblonga; legumen juvenile tenue, glabratum, inter semina constrictum.

A small tree, about 2 meters high, the twigs terete, with scanty spreading hairs when young, soon becoming glabrous. Petiole and rachis slender, about 5 cm. long; stipules minute, narrow; leaflets oblong-lanceolate, 3–7 cm. long, acuminate. glabrous on both sides, shining above, an oblong gland between the lower pair: inflorescence axillary; peduncles slender, sometimes as long as the leaves; pedicels slender. 2–3 cm. long; sepals 5 mm. long; petals oblong, about 12 mm. long; ovary at first pubescent, soon glabrate; young legume slender, glabrate, about 7 cm. long. constricted between the seeds.

Cuesta de Tocotá, road from Buenaventura to Cali, El Valle, Colombia, December, 1905, *Pittier 720*, type (U.S.).

12. Chamæfistula Curranii Rose, sp. nov.

Arbor, ramulis inflorescentiaque puberulis; rachidis glandula inter jugum inferius foliolorum; foliola membranacea, glabra, subabrupte acuminata, subinæquilateralia, inferiora ovata vel ovato-elliptica, superiora anguste obovata; inflorescentia laxe paniculata, pedicellis tenuissimis; sepala acuta.

A tree, about 5 m. high, the slender twigs and the inflorescence puberulent. Leaf-rachis sparingly pubescent, bearing a gland between the lower pair of leaflets: leaflets membranous, glabrous, rather abruptly acuminate, slightly inequilateral, the lower pair ovate or ovate-elliptic. 8–10 cm. long, the upper pair narrowly obovate, somewhat longer than the lower; inflorescence loosely paniculate: pedicels very slender, 2–3 cm. long; sepals ovate, acute, puberulent, 6–7 mm. long: petals about 12 mm. long (perhaps longer).

Vicinity of Estrella, Caño Papayal, Lands of Loba, Bolívar, Colombia, April–May, 1916, *H. M. Curran 348*, type (U.S.). Donama, Magdalena, *Giacometto 50*. Magdalena Valley, *Allen 431*.

13. Chamæfistula oxyphylla (Kunth) G. Don, Gen. Syst. 2: 451. 1832.

Cassia oxyphylla Kunth, Mim. 129, *pl. 39*. 1819.

Type locality: Cocollar, Venezuela.
Santa Marta, *H. H. Smith 253*. Sitio nuevo, Magdalena Valley, *André 215*. Venezuela.

14. Chamæfistula speciosa (Schrad.) G. Don, Gen. Syst. 2: 451. 1832.

Cassia speciosa Schrad. Goett. Anz. 1821: 718. 1821.

Type locality: Brazil.
Caquezá, Cundinamarca, *Pennell 1895*. Dept. Santander, *Killip & Smith 14919, 15403, 15415, 16459, 16828, 19447*. Without locality, *Mutis 2055, 1099*. Brazil.

15. Chamæfistula subcoriacea Britton & Killip, sp. nov.

Arbor parva. ramulis sparse strigosis, mox glabratis; rachis strigosa, glandula oblonga, obtusa, inter jugum inferius foliolorum; foliola subcoriacea, oblique elliptica vel ovato-elliptica, dense reticulata, supra laxe appresso-pubescentia vel glabrata, subtus subtomentosa; inflorescentia subterminalis, compacta, pauciflora: sepala elliptica; petala suborbicularia.

A small tree, 3–5 mm. high. the twigs sparingly strigose, soon glabrous. Petioles stout, 1–2 cm. long; rachis short. strigose, only 5–15 mm. long, bearing

an oblong blunt gland between the lower leaflets; leaflets subcoriaceous, obliquely elliptic to ovate-elliptic, finely reticulate-veined, loosely appressed-pubescent or glabrate above, subtomentose beneath, the apex acute or obtuse, the upper pair 5–8 cm. long; inflorescence borne in the upper axils and subterminal, compact, few-flowered; pedicels strigose, 1–2.5 cm. long; sepals elliptic, 5 mm. long, rounded; petals suborbicular, about 13 mm. long; young legume sparingly strigose.

Open hillside, upper Río Lebrija Valley, Santander, Colombia, 400–700 m. altitude, December 29, 1926, *Killip & Smith 16276*, type (N.Y.).

16. Chamæfistula apiculata Britton & Killip, sp. nov.

Fere ubique glabra; glandulæ conicæ, obtusæ, inter juga ambo foliolorum; foliola elliptica, chartacea, obtusa et apiculata, subtus in venis puberula; inflorescentia axillaris et terminalis, subracemosa, puberula; sepala oblonga.

Branches slender, glabrous. Petiole and rachis glabrous, slender: glands conic, blunt, about 2 mm. long, borne between both pairs of leaflets: leaflets elliptic, chartaceous, pale, and puberulent on the veins beneath, glabrous and light green above, the apex obtuse, apiculate, the base rounded or obtuse, the upper pair 6–9 cm. long, 3–5 cm. wide, the lower pair smaller; inflorescence axillary and terminal, subracemose, puberulent, few-several-flowered: pedicels very slender, 1–3.5 cm. long; sepals oblong, rounded, 4–6 mm. long; petals about 1.5 cm. long: anthers 8 mm. long.

Titiribí, vicinity of Medellín, Colombia, *R. 4. Toro 419*, type (N.Y.). Without locality, *Mutis 4725*, referred here with hesitation.

17. Chamæfistula Toroana Britton & Killip, sp. nov.

Rami minute puberuli; rachis inter jugum inferius foliolorum glandulosa; foliola membranacea, ovata vel elliptica vel obovata, supra sparse strigillosa, subtus glabrescentia; inflorescentia racemoso-paniculata, puberula; sepala breviter elliptica vel ovato-elliptica, puberula; legumen glabrum.

Branches slender, finely puberulent. Petioles rather stout, sparingly puberulent, 2–4 cm. long; rachis bearing a small blunt gland about 2 mm. long between the lower pair of leaflets; leaflets membranous, various, ovate to elliptic or obovate, acutish or obtuse (or the lower pair acuminate), dark green and sparing strigillose above, light green and glabrous or nearly so beneath, the upper pair 8–16 cm. long; inflorescence racemose-paniculate, terminal and in the upper axils, 8–12 cm. long, its branches and the pedicels puberulent; sepals short-elliptic to ovate-elliptic, 3–4 mm. long, puberulent, rounded; petals about 15 mm. long: legume glabrous, 10–12 cm. long, about 12 mm. thick.

Fredonia, vicinity of Medellín, Colombia, December 20, 1927, *Toro 848*, type (N.Y.). Popayán, *Lehmann 8478*.

18. Chamæfistula inæquilatera (Balbis) G. Don, Gen. Syst. 2: 451. 1832.

Cassia inæquilatera Balbis; DC. Prodr. 2: 490. 1825.

Type locality : Santa Marta, Colombia.
Santa Marta, *Bertero* (photograph of type); *H. H. Smith 700*. Venezuela.

19. Chamæfistula tolimensis Britton & Rose, sp. nov.

Arbor glabra, ramis subflexuosis; rachidis glandula oblonga, obtusa, inter jugum inferius foliolorum: foliola chartacea, oblique ovata, acuta vel obtusa; inflorescentia terminalis, laxiflora; legumen ad basim apicemque angustatum.

A glabrous shrub, the slender branches somewhat flexuous. Petiole rather stout, 1–2 cm. long; rachis bearing an oblong obtuse gland between the lower pair of leaflets; leaflets chartaceous, obliquely ovate, acute or obtuse, green on both sides but slightly paler beneath than above, 4–9 cm. long; inflorescence terminal, loosely several-flowered; pedicels about 2 cm. long, or shorter; petals

about 1 cm. long; legume 2.4 dm. long, 8 mm. wide, narrowed at base and apex, delicately reticulate-veined.

Edge of forest, Honda, Tolima, Colombia, 300-500 m. altitude, January 3, 4, 1918, *Pennell 3559*, type (N.Y.).

20. Chamæfistula bolivarensis Britton & Rose, sp. nov.

Frutex, ramulis flexuosis, puberulis; rachidis glandula magna, obtusa, inter jugum inferius foliolorum; foliola ovata vel ovato-lanceolata, chartacea, acuta vel acuminata, supra glabrata, subtus pubescentia; panicula terminalis, multiflora, floribus dense puberulis; legumen juvenile dense puberulum, crasse reticulatum.

A shrub with zigzag puberulent twigs. Petioles puberulent, 1-2 cm. long; rachis 2-3 cm. long, bearing a large obtuse gland between the lower pair of leaflets; leaflets ovate to ovate-lanceolate, acute or acuminate, pale on both sides. glabrate above, strongly veined and pubescent beneath, the upper pair 7-12 cm. long, the lower pair much smaller; inflorescence a terminal many-flowered panicle; pedicels pubescent, about 2 cm. long; sepals and petals densely puberulent; petals pale yellow, about 1 cm. long; ovary densely appressed-pubescent; young legume about 30 cm. long and 6 mm. wide, densely puberulent, coarsely and irregularly reticulate-veined.

Tierra Alta, Río Sinú, Bolívar, Colombia, March 7-10, 1918, *Pennell 4666*, type (N.Y.).

21. Chamæfistula bacillaris (L. f.) G. Don, Gen. Syst. 2: 241. 1832.

Cassia bacillaris L.f. Suppl. 231. 1781.
Cassia puberula H.B.K. Nov. Gen. & Sp. 6: 341. 1824.
Chamœfistula puberula G. Don, Gen. Syst. 2: 441. 1832.
Cassia carthaginensis Willd.; Steud. Nom. ed. 2, 304. 1840.

Type locality: Surinam.
Frequent in Colombia. Venezuela, Trinidad and Tobago to Surinam and Brazil; Panama; Costa Rica; St. Vincent; Puerto Rico.

22. Chamæfistula micradenia Britton & Killip, sp. nov.

Frutex glaber: rachidis glandula globosa, parva, inter jugum inferius foliolorum; foliola ovata. subchartacea, obtuse acuminata, subæquilateralia; legumen brevistipitatum, obtusum, in medio depressum.

A glabrous shrub with slender twigs. Leaf rachis 6-8 cm. long, bearing a globose gland only 2 mm. in diameter between the lower pair of leaflets; leaflets ovate, subchartaceous, gradually bluntly acuminate, pinnately few-veined and rather densely reticulated. 7-10 cm. long, nearly equilateral; inflorescence not seen; fruiting pedicels about 4.5 cm. long, rather stout; legume about 20 cm. long, and 15 mm. broad, short-stipitate, blunt, with a narrow. depressed median area.

In forest, La Virginia, Líbano, Tolima, Colombia, 1200-1500 m. altitude, December 22, 1917, *Pennell 3278*, type (N.Y.).

Although annotated by the collector as having pale sulphur-yellow petals, no flowers accompany the specimen.

22. ADIPERA Raf. Sylva Tell. 129. 1838.

Type species: *Cassia Herbertiana* Lindl.

KEY TO SPECIES OF ADIPERA

Glabrous. or very nearly so throughout.
Leaflets long-acuminate .... 1. *A. lævigata.*
Leaflets rounded or obtuse.................... 2. *A. bicapsularis.*

Branches and inflorescence more or less densely
    pubescent, or velutinous.
    Leaflets obovate, rounded; three of the anthers
        long-beaked.
        A shrub; petals 10–12 mm. long; leaf-gland
            cylindric, or clavate................... 3. *A. indecora.*
        A tree; petals much larger; leaf-gland
            subglobose .... 4. *A. arborea.*
    Leaflets oblong or lanceolate.
        Leaflets oblong. obtuse or acute........... 5. *A. tomentosa.*
        Leaflets lanceolate, acuminate............. 6. *A. santanderensis.*

1. **Adipera lævigata** (Willd.) Britton & Rose; Britton & Wilson, Sci. Surv.
   Porto Rico & Virgin Ids. 5 : 371. 1924.

   Cassia lævigata Willd. Enum. 441. 1809.

   Type locality : Not cited.
   Medellín, *Toro 561.* Villavicencio, Meta, *Triana 4379.* Guiana (according to Bentham) ; Sinaloa to Guatemala ; Cuba ; Puerto Rico ; Jamaica.   Old World tropics.

2. **Adipera bicapsularis** (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto
   Rico & Virgin Ids. 5 : 370. 1924.

   Cassia bicapsularis L. Sp. Pl. 376. 1753.
   Cassia pendula Willd. Enum. 440. 1809.

   Type locality : India.
   Frequent in Colombia.   Tropical and subtropical America. north to Bermuda,
   Florida and Sinaloa.   Old World tropics.   PLATANITO, BOMBITO, BICHO, COMIDA DE
   MURCIÉLAGO, COIJOL.

3. **Adipera indecora** (H.B.K.) Britton & Rose, N. Am. Flora 23 : 239. 1930.

   Cassia indecora H. B. K. Nov. Gen. & Sp. 6 : 344. 1824.

   Type locality : Caracas, Venezuela.
   Frequent, or occasional, in Colombia.   Brazil to Trinidad ; Panama and Tepic ;
   Cuba ; Hispaniola.   Canary Islands.   ALCAPARRO.

4. **Adipera arborea** Britton & Killip, sp. nov.

   Arbor dense et breviter pubescens; foliola 3–4-juga, oblongo-obovata, membranacea, rotundata, supra glabra, subtus dense strigosa, glandula subglobosa ; racemi terminales et axillares ; sepala obtusa, laxe strigosa ; petala obovata.

   A tree, 4–6 m. high. the branches, petioles, rachis and inflorescence densely short-pubescent.   Petioles 1–3 cm. long ; rachis bearing a subglobose gland between the lowest pair of leaflets ; leaflets 3 or 4 pairs, oblong-obovate, membranous, distantly pinnately veined, rounded, dark green and glabrous above, densely strigose beneath, the upper pairs 2.5–3.5 cm. long, the lower smaller ; racemes terminal and axillary, several-flowered, on stout peduncles 10 cm. long, or shorter ; pedicels 1–1.5 cm. long ; sepals obtuse, loosely strigose, about 12 mm. long ; petals obovate, glabrous, bright yellow, 15–18 mm. long ; three of the anthers long-beaked.

   Mesa de los Santos. 1500 m. altitude, Santander, Colombia, December 12, 1926,
   Killip & Smith 15180, type (N.Y.).

5. **Adipera tomentosa** (L. f.) Britton & Rose, N. Am. Flora 23 : 241. 1930.

   Cassia tomentosa L. f. Suppl. 231. 1781.

   Type locality : South America.
   Frequent in Colombia.   Argentina and Chile to Bolivia and Ecuador ; Guatemala to
   Hidalgo, Mexico.   ALCAPARRO.

6. Adipera santanderensis Britton & Killip, sp. nov.

Frutex dense flavo-pubescens; rachidis glandula subcylindrica, acuta, inter jugum inferius foliolorum; foliola 4–5-juga, lanceolata, acuta vel breviter acuminata, supra glabra, subtus laxe pubescentia; flores racemosi, axillares et terminales: sepala subelliptica, obtusa vel rotundata; petala obovata; stamina 7; staminodia 3; legumen lineare, planum, sparse pubescens.

A shrub, 3–4 m. high, the branches, petioles, rachis and inflorescence densely yellowish-pubescent. Petioles 1.5–2 cm. long; rachis bearing a subcylindric pointed gland about 2 mm. long between the lower pair of leaflets; leaflets 4 or 5 pairs, lanceolate, acute or short-acuminate, 3–4.5 cm. long, glabrous above, loosely pubescent beneath, the base rounded; flowers racemose, axillary and terminal; peduncle stout, 5–7 cm. long; pedicels slender, 1–2 cm. long; sepals nearly elliptic, obtuse or rounded, 9–13 mm. long; petals obovate, yellow, delicately veined, about 15 mm. long: stamens 7, the longer anthers about 9 mm. long; staminodes 3: ovary densely yellowish-strigose; legume linear, flat, sparingly pubescent, about 7 cm. long and 8 mm. wide.

Santander and Norte de Santander, Colombia. Type from clearing, Río Suratá Valley, above Suratá, Santander, at 2000 to 2300 m. elevation, January 6, 1927, *Killip & Smith 16697*, type (N.Y.). Santander, *Killip & Smith 16101, 16886, 18397, 19224, 19518*. Tapatá, Norte de Santander, *Killip & Smith 20495*.

23. EMELISTA Raf. Sylva Tell. 127. 1838.

Type species: *Cassia obtusifolia* L.

KEY TO SPECIES OF EMELISTA

Glabrous, or nearly so, throughout.................. 1. *E. Tora.*
Stems, petioles and legumes long-pilose............. 2. *E. pilifera.*

1. Emelista Tora (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 371. 1924.

Cassia Tora L. Sp. Pl. 376. 1753.
Cassia obtusifolia L. Sp. Pl. 377. 1753.

Type locality: India.
Common in Colombia. Nearly cosmopolitan in tropical and warm-temperate regions, in America ranging north to Pennsylvania and Missouri. BICHO, CHILINCHILE.

2. Emelista pilifera (Vogel) Pittier, Journ. Wash. Acad. Sci. 19: 176. 1929.

Cassia pilifera Vogel, Syn. Cass. 23. 1837.

Type locality: Brazil.
Ocaña, Norte de Santander, *Schlim 268*. Bolivia to Brazil and Argentina: Panama to Veracruz and Durango; Cuba.

24. HERPETICA Raf. Sylva Tell. 123. 1838.

Type species: *Cassia alata* L.

1. Herpetica alata (L.) Raf. Sylva Tell. 123. 1838.

Cassia alata L. Sp. Pl. 378. 1753.

Type locality: South America.
Medellín, *Toro 422*. Quibdó, El Chocó, *Archer 1754, 1818*. Timbiquí, El Cauca, *Lehmann B.T.372*. Huila, *Rusby & Pennell 278*. Venezuela to French Guiana, Bolivia and Paraguay; Panama to Guerrero; West Indies (except Bahamas). Old World tropics. MARTINGALBE, BAJAGUA, LUCUTEMA, MAJAGUILLO, MOCUTENO, YERBA DE PLAYA.

25. CHAMÆSENNA Raf.; Pittier, Arb. & Arb. Legum. 130. 1928.

Type species: *Cassia reticulata* Willd.

KEY TO SPECIES OF CHAMÆSENNA

Upper leaflets obovate............................ 1. *C. reticulata.*
Leaflets all oblong or lanceolate.

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Leaflets oblong, rounded or obtuse.
  Leaves and twigs glabrous; inflorescence
      sparingly pubescent ..................  2. C. colombiana.
  Leaflets floccose-pubescent beneath; twigs
      and inflorescence densely pubescent.....  3. C. pistaciæfolia.
  Leaflets lanceolate, acuminate; twigs and inflores-
      cence velvety-pilose ......................  4. C. velutina.
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1. Chamæsenna reticulata (Willd.) Pittier, Arb. & Arb. Legum. 130. 1928.

Cassia reticulata Willd. Enum. 443. 1809.
Cassia strobilacea H. B. K. Nov. Gen. & Sp. 6: 347. 1824.

Type locality: Pará, Brazil.
Frequent in Colombia. Brazil to Bolivia, Trinidad and Ecuador ; Panamá to Guatemala. DORONCEL, DORANCÉ.

2. Chamæsenna colombiana Britton & Killip, sp. nov.

Arbor glabra. racemis exceptis; foliola 4–6-juga, oblongo-elliptica. chartacea, ambitu obtusa vel rotundata ; racemi axillares, foliis multo longiores; sepala oblique elliptica vel obovata, ciliata; petala obovata; stamina 7–8; legumen late lineare, transverse rugosum.

A tree with glabrous twigs and leaves, the racemes loosely pubescent. Petiole and leaf-rachis 10–16 cm. long; leaflets 4–6 pairs, oblong-elliptic, chartaceous, 5–9 cm. long, obtuse, or rounded at both ends, loosely reticulate-veined, faintly shining above, dull beneath; racemes axillary, much longer than the leaves, several-many-flowered: pedicels slender, 10–15 mm. long; bractlets 4–6 mm. long, fugacious; sepals obliquely elliptic to obovate, rounded. parallel-veined, ciliate, 10–12 mm. long; petals yellow, obovate, rounded, strongly veined, a little longer than the sepals; stamens 7 or 8, the 2 larger ones with anthers about 7 mm. long, the others with anthers about one-half as long: style strongly curved; legume broadly linear, thin, flat, glabrous, narrowed at base, 7–9 cm. long, 15–18 mm. wide, transversely ridged, its narrow margins slightly thickened.

Vicinity of Medellín, Colombia. Type from Boquerón, January 5, 1928, *Toro 866*, type (N.Y.) Cucaracho, Antioquia, December 25, 1927, *Toro 839.* Antioquia, *Jervise; Triana.*

3. Chamæsenna pistaciæfolia (H.B.K.) Britton.

Cassia pistaciæfolia H. B. K. Nov. Gen. & Sp. 6: 349. 1824.

Type locality : Between Popayán and Meneses. Colombia.
Popayán, *Lehmann 7793, 8539.* Puracé, El Cauca, *Pennell & Killip 6445.* Bogotá, *Cuatrecasas 3165.* Endemic.

4. Chamæsenna velutina Britton & Killip, sp. nov.

(See PLATE II.)

Arbor, ramulis petiolis rachidibusque velutinis ; petioli eglandulosi ; foliola 4–6-juga, late lanceolata, acuminata, subchartacea, supra glabrata. subtus pubescentia; racemi laxiflori; sepala elliptico-obovata; petala late obovata; stamina 7–8; legumen late lineare, glabrum.

A tree, 3–4 m. high, branched above. the trunk about 1 dm. in diameter, the twigs, petioles and leaf-rachis densely velvety-pilose. Stipules triangular-lanceolate, acuminate, pubescent, 1.5–2 cm. long; petioles stout. eglandular, 5 or 6 cm. long; leaflets 4–6 pairs, broadly lanceolate, acuminate, subchartaceous, pinnately veined, 7–12 cm. long, 3–4 cm. wide, nearly glabrous above. pubescent beneath; peduncles stout, sparingly pubescent, about 15 cm. long: raceme loosely several-flowered, about 10 cm. long, the rachis sparingly pubescent; pedicels slender, glabrate, 1–2 cm. long; sepals elliptic-obovate, glabrous, striate-veined, obtuse, 12–18 cm. long; petals broadly obovate, yellow, strongly color-veined, a

little longer than the sepals; stamens 7 or 8, the anthers of the 3 larger ones curved, 17–20 mm. long: legume broadly linear, glabrous, flat, irregularly, transversely reticulate-veined, about 11 cm. long and 2 cm. wide, the seeds not elevated.

Plaza, *Mutiscua*, Norte de Santander, Colombia, 2600 m. altitude, February 20, 1927, *Killip & Smith 19655*, type (N.Y.). Bogotá, *Popenoe 11½*.

26. SCIACASSIA Britton; Britton & Rose, N. Am. Flora 23: 252. 1930.

Type species: *Cassia siamea* Lam.

1. Sciacassia siamea (Lam.) Britton; Britton & Rose, N. Am. Flora 23: 252. 1930.

Cassia siamea Lam. Encycl. 1: 648. 1785.
Cassia florida Vahl, Symb. 3: 57. 1794.

Type locality: Siam.
Vicinity of Cartagena, *Heriberto 189*. Widely planted for shade in tropical America. Native of the East Indies.

27. DITREMEXA Raf. Sylva Tell. 127. 1838.

Type species: *Cassia occidentalis* L.

KEY TO SPECIES OF DITREMEXA

Legume very narrow, 10–30 cm. long, 3–5 mm. wide,
    pubescent or glabrate; seeds oblique .... 1. *D. leptocarpa.*
Legume shorter, wider; seeds transverse.
    Legume densely hirsute, 5–7 mm. wide.......... 2. *D. hirsuta.*
    Legume glabrous or sparingly pubescent.
        Legume flat, somewhat curved............. 3. *D. occidentalis.*
        Legume turgid, straight................... 4. *D. Sophera.*

1. Ditremexa leptocarpa (Benth.) Britton & Rose, N. Am. Flora 23: 256. 1930.

Cassia leptocarpa Benth. Linnæa 22: 528. 1849.

Type locality: Zapativa, Brazil.
Popayán, *Lehmann 5511, 536½*. Cisneros, El Valle, *Killip 5369*. Vicinity of Medellín, *Toro 7, 48, 70, 671*. Without locality, *Triana 454*. Venezuela to Brazil and Paraguay; El Salvador to Tepic and Veracruz; Cuba.

2. Ditremexa hirsuta (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 372. 1924.

Cassia hirsuta L. Sp. Pl. 378. 1753.

Type locality: America.
Fusagasugá, Cundinamarca, *André 1½79*. Tolima, *Pennell 33½6*. Trinidad to Surinam, Ecuador and Argentina; El Salvador; Jamaica; Puerto Rico; Lesser Antilles.

3. Ditremexa occidentalis (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 372. 1924.

Cassia occidentalis L. Sp. Pl. 377. 1753.

Type locality: Jamaica.
Common in Colombia. Tropical and temperate America, north to Virginia and Texas. Old World tropics. CHILINCHILE, BRUSCA, POTRA, GALLINAZO, BICHO DE CAFÉ, BICHO LARGO.

4. Ditremexa Sophera (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 372. 1924.

Cassia Sophera L. Sp. Pl. 379. 1753.

Type locality: India.
Medellín, *Toro 8½*. Venezuela; Curaçao; Panama; Veracruz; West Indies. Old World tropics.

28. PEIRANISIA Raf. Sylva Tell. 127. 1838.

Type species: *Cassia aversiflora* Hook.

KEY TO SPECIES OF PEIRANISIA

Leaflets 30–50 pairs; branches long-pilose and pubescent .... 1. *P. Mutisiana.*
Leaflets 3–7 pairs.
    Leaflets densely pubescent beneath.
        A gland borne between most of the pairs of
            leaflets .... 2. *P. santandcrensis.*
        A gland borne between 1 or 2 of the lower
            pairs of leaflets...................... 3. *P. velutina.*
    Leaflets glabrous or sparingly pubescent.
        Leaflets obtuse or mucronate.............. 4. *P. biflora.*
        Leaflets abruptly awned .... 5. *P. aristulata.*

1. Peiranisia Mutisiana (Kunth) Pittier, Arb. & Arb. Legum. 128. 1928.

Cassia Mutisiana Kunth, Mim. 142, *pl. 43.* 1819.

Type locality: New Grenada.
Santander, *Killip & Smith 16400, 19404.* Norte de Santander, *Killip & Smith 19807.* Cundinamarca, *Triana 4403; Rusby & Pennell 850; Pérez 2535.* Quindío Trail, Tolima, *Killip & Hazen 9631.* Without locality, *Mutis 2394, 4214* (co-type). Venezuela.

2. Peiranisia santanderensis Britton & Killip, sp. nov.

Frutex vel arbor parva, ramulis dense et breviter pubescentibus; foliola 4–7-juga, oblonga, obtusa vel acuta, membranacea, supra laxe et breviter pubescentia, subtus dense pilosa, glandulis oblongo-subclavatis, inter juga plurima foliolorum; racemi pilosi; sepala suborbiculata.

A shrub or small tree 3–5 m. high, the twigs rather densely short-pubescent. Leaflets 4–7 pairs, membranous, oblong, obtuse or acute, mucronulate, loosely short-pubescent above, densely appressed-pilose beneath, the upper ones 2.5–4 cm. long, the lower ones shorter; glands oblong-subclavate, 1–1.5 mm. long, borne between most of the pairs of leaflets; racemes few-several-flowered, pilose; pedicels 2 cm. long, or shorter; sepals suborbicular, 3–5 mm. long, sparingly pubescent below; petals 1.5–2 cm. long; three of the anthers long-beaked; young legume about 10 cm. long and 2.5 mm. wide, sparingly appressed-pubescent.

Open hillside, between Pamplonita and Chinácota, Río Pamplonita Valley, Norte de Santander, Colombia, 1300–1800 m. altitude, March 17, 1927, *Killip & Smith 20750,* type (N.Y.). Ocaña, *Schlim 2,* referred by Bentham to the Cuban species *Cassia robiniæfolia* (Benth.).

3. Peiranisia velutina Britton & Killip, sp. nov.

Frutex, ramulis inflorescentiaque dense vel laxe pilosis; foliola 4–7-juga, membranacea, oblonga, elliptica vel (suprema) oblanceolata, supra brevipubescentia, subtus dense appresso-pilosa, glandula clavata, inter jugum inferius; racemi pauciflori, pedunculis 1–2-floris; sepala elliptica vel suborbiculata; legumen anguste lineare, appresso-pubescens.

A shrub about 3 m. high, the twigs and inflorescence densely or loosely short-pilose, the twigs slender. Leaflets 4–7 pairs, membranous, oblong, elliptic, or the upper pair oblanceolate, rounded or obtuse, 1–2.5 cm. long, short-pubescent above, densely appressed-pilose beneath; gland clavate, slender, about 2 cm. long, borne between the lowest pair of leaflets; racemes few-flowered; pedicels densely pilose; peduncles 1-or-2-flowered; sepals elliptic to suborbicular, glabrate, 5–7 mm. long; petals 1.5–1.8 cm. long; two or three of the anthers long-beaked; legume narrowly linear, appressed-pubescent, 8–14 cm. long, 3.5–5 mm. wide, its stipe about 6 mm. long.

Patía Valley, Nariño, Colombia, 200–500 m. altitude, *Lehmann B.T.832,* type (N.Y.); *Lehmann 7792; Lehmann B.T.827.*

4. **Peiranisia biflora** (L.) Pittier, Arb. & Arb. Legum. 128. 1928.

   Cassia biflora L. Sp. Pl. 378. 1753.
   Cassia pallida Vahl, Eclog. 3: 12. 1807.

   Type locality: Unknown: species described from a cultivated plant.
   Frequent at lower altitudes in northern Colombia. Venezuela: Grenada; Cuba; Bahamas; Costa Rica to Sinaloa and Chihuahua. BOMBITO, BICHO, ESCOVITO.

5. **Peiranisia aristulata** Britton & Killip, sp. nov.

   Fere ubique glabra; rachidis glandula tenuis, inter jugum infimum foliolorum; foliola 6–10-juga, oblonga vel (suprema) anguste obovata, membranacea, obtusa. aristulata; inflorescentia racemoso-paniculata, appresso-pubescens; flores parvi; sepala suborbiculata, ciliolata.

   Twigs slender, glabrous, elongated; leaves rather distant, about 10 cm. long, or shorter, the petiole about 2 cm. long, the slender rachis sparingly appressed-pubescent, bearing a slender gland 2–3 mm. long between the lowest pair of leaflets: leaflets 6–10 pairs, oblong (or the upper ones narrowly obovate), membranous, glabrous, dull, 1.5–2 cm. long, 3–6 mm. wide. delicately pinnately few-veined, the obtuse base slightly oblique, the apex obtuse, with the midvein produced into a filiform bristle about 1 mm. long; inflorescence racemose-paniculate. appressed-pubescent, in bud about 5 cm. long, or shorter, its branches about 2.5 cm. long. or shorter, bearing few, nearly sessile, small flowers; bractlets linear to nearly filiform, longer than the young calyx: sepals suborbicular, ciliolate.

   Villavicencio, Meta, Colombia, December, 1928, *Apollinaire Marie,* type (Herb. Instituto de la Salle, Bogotá).

   Peiranisia riciæfolia (Benth.) Pittier (*Cassia riciæfolia* Benth.) was erroneously reported from Colombia by Bentham, on the basis of Fendler specimens actually collected in Venezuela. Micheli, however, refers to it André's 2744bis. from the Cauca Valley, a specimen we have not seen.

29. ISANDRINA Raf. Sylva Tell. 126. 1838.

Type species: *Cassia emarginata* L.

1. **Isandrina emarginata** (L.) Britton & Rose; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 374. 1924.

   Cassia emarginata L. Sp. Pl. 376. 1753.

   Type locality: Caribbean Islands.
   Frequent in northern Colombia, at lower elevations. Venezuela; Ecuador; Greater Antilles; Guadeloupe; Costa Rica to Sonora and Tamaulipas. CHIHUCTO, CHIVATO, CARANGANETO.

30. CHAMÆCRISTA Moench, Meth. 272. 1794.

Type species: *Cassia Chamæcrista* L.

KEY TO SPECIES OF CHAMÆCRISTA

A. Sepals rigid, delicately many-nerved; leaflets 1 or
   2 pairs. (UNIFLORE)
   Leaflets 1 pair.................................... 1. *C. cultrifolia.*
   Leaflets 2 pairs.
      Leaflets obovate: legume appressed-pubescent.... 2. *C. tetraphylla.*
      Leaflets oblong, linear. or oblanceolate.
         Leaflets oblong to oblanceolate.
            Leaflets 8–12 mm. long; legume glabrous, or
               nearly so, narrow..................... 3. *C. Persoonii.*
            Leaflets 12–20 mm. long; legume pubescent.
               broad .... 4. *C. pulchra.*

Leaflets linear .... 5. *C. Lehmannii.*
B. Sepals not rigid, not delicately many-nerved.
Midvein of the leaflets marginal. (TRISTICULÆ).. 6. *C. tristicula.*
Midvein of the leaflets subcentral or excentric.
1. Prostrate or ascending, slender herbs.
Legume short, 1–4-seeded; leaflets 2 or 3 pairs,
obcuneate. (TAGERÆ)
Flowers filiform-peduncled; legume oblong. 7. *C. Tagera.*
Flowers short-peduncled; legume linear.... 8. *C. Schlimii.*
Legume linear, several-seeded.
Leaflets 1 pair, broadly obovate; flowers
filiform-peduncled. (ROTUNDIFOLIÆ)
Leaflets 1–2 cm. long; legume 2–3 cm. long. 9. *C. rotundifolia.*
Leaflets 3–4 cm. long; legume 4–6 cm. long. 10. *C. bauhiniæfolia.*
Leaflets 3–20 pairs, linear to oblong.
Branches long-pilose; petiole eglandular;
flowers filiform-peduncled. (PILOSÆ) 11. *C. pilosa.*
Branches puberulent or glabrate; petiole
glanduliferous. (SERPENTES)
Petiolar gland slender, long-stalked.
Leaflets 4–9 pairs, linear-oblong.
Stipules narrowly lanceolate...... 12. *C. serpens.*
Stipules broadly ovate, cordate.... 13. *C. supplex.*
Leaflets 8–20 pairs, narrowly linear. 14. *C. trichopoda.*
Petiolar gland sessile................ 15. *C. Pennellii.*
2. Shrubs or perennial herbs, mostly erect.
Leaflets 15–50 pairs; stem flexuous. (FLEX-
UOSÆ) .... 16. *C. flexuosa.*
Leaflets fewer; stems not flexuous.
a. Leaflets membranous, linear to linear-
oblong, narrow; low shrubs. (PATEL-
LARIÆ)
*Petiolar gland sessile, flat or concave.
Petiolar gland oblong, 2.5 mm. long.... 17. *C. Browniana.*
Petiolar gland orbicular, much smaller.
Leaflets 5–8 mm. long, glabrous...... 18. *C. simplex.*
Leaflets 8–15 mm. long, pubescent.... 19. *C. patellaria.*
**Petiolar gland stalked.
Stem pilose-pubescent.
Leaves pilose .... 20. *C. flavicoma.*
Leaves glabrous .... 21. *C. stenocarpa.*
Stem appressed-pubescent or puberulent. 22. *C. riparia.*
b. Leaflets chartaceous, broader.
Leaflets closely many-veined. (LINEATÆ) 23. *C. Andreana.*
Leaflets not closely veined; shrub 3–4 m.
high. (ARBORESCENTES) .... 24. *C. arborescens.*

1. Chamæcrista cultrifolia (H. B. K.) Britton & Rose.

Cassia cultrifolia H. B. K. Nov. Gen. & Sp. 6: 363. 1824.

Type locality: Orinoco River.
Colombia, *Mutis 1277.* Venezuela; Brazil.

2. Chamæcrista tetraphylla (Desv.) Britton & Rose.

Cassia tetraphylla Desv. Journ. Bot. 3: 72. 1814. Not Collad. 1816.
Cassia Desvauxii Collad. Hist. Cass. 131. 1816.

Type locality: Tropical America.
Colombia, *Burke 299; Bruckmüller.* British Guiana; Brazil.

3. **Chamæcrista Persoonii** (Collad.) Greene, Pittonia 4: 31. 1899.

Cassia uniflora Spreng. Neue Entd. 1: 291. 1820. Not Mill., 1768.
Cassia Persoonii Collad. Hist. Cass. 119. 1816.

Type locality: Cayenne.
Colombia (according to Bentham). Venezuela to French Guiana and Brazil.

4. **Chamæcrista pulchra** (H. B. K.) Britton & Rose.

Cassia pulchra H. B. K. Nov. Gen. & Sp. 6: 362. 1824.

Type locality: Near San Carlos on the Río Negro. Venezuela.
Santander, *Killip & Smith 15089, 15127, 193 \(\frac{1}{3}\)5.* Brazil; Honduras.

5. **Chamæcrista Lehmannii** Britton & Rose, sp. nov.

Frutex ramosissimus, ramulis dense puberulis; stipulæ ovatæ, plurinerviæ; petiolorum glandula sessilis, orbiculata, subplana; foliola 2-juga. linearia, multinervia, glabra, ciliolata, obtusa; pedunculi solitarii; sepala lanceolata, multinervia; petala obovata; stamina 10.

A much-branched, densely leafy shrub, at least 3 dm. high, the slender twigs densely puberulent. Stipules ovate, cordate, acute, 5–7 mm. long, many-nerved; petioles about 5 mm. long, bearing a small, sessile, orbicular, nearly flat gland just below the lower pair of leaflets; rachis very short, subulate-tipped; leaflets 2 pairs, approximate, linear, 1.5–2 cm. long, many-veined, glabrous but ciliolate, the apex obtuse; peduncles solitary, slender, 1.5–2 cm. long, pilose; bracts at the base of the calyx broadly ovate to orbicular, many-nerved; sepals lanceolate. acuminate, many-nerved. 10–12 mm. long; petals obovate, about as long as the sepals, or shorter; stamens 10.

Guagua, Huila. Colombia, *Lehmann B.T.1095,* type (N.Y.).

6. **Chamæcrista tristicula** (H. B. K.) Britton & Rose.

Cassia tristicula H. B. K. Nov. Gen. & Sp. 6: 367. 1824.

Type locality: Fusagasugá, Colombia.
Cundinamarca, *Pennell 1328, 1869; Humboldt & Bonpland* (type). Without locality, *Mutis 2388.*

7. **Chamæcrista Tagera** (L.) Standley, Contr. U. S. Nat. Herb. 18: 104. 1914.

Cassia Tagera L. Sp. Pl. 376. 1753.

Type locality: India (presumably in error).
Colombia (according to Bentham); Guiana (according to Bentham); Brazil; Panama to Veracruz.

8. **Chamæcrista Schlimii** (Benth.) Britton & Rose.

Cassia Schlimii Benth. Trans. Linn. Soc. 27: 571. 1871.

Type locality: Ocaña, Colombia.
Ocaña, Norte de Santander, *Schlim 281.* Sincé, Bolívar, *Pennell 4009.* Rincón Hondo, Magdalena, *Allen 264.* Endemic.

9. **Chamæcrista rotundifolia** (Pers.) Greene, Pittonia 3: 41. 1899.

Cassia rotundifolia Pers. Syn. 1: 456. 1805.

Type locality: South America.
Villavicencio, Meta, *Apollinaire Marie.* San Martín, Meta, *Shaw.* Venezuela to the Guianas, Bolivia and Brazil; Costa Rica to Sinaloa; Cuba.

10. **Chamæcrista bauhiniæfolia** (Kunth) Britton & Rose.

Cassia bauhiniæfolia Kunth, Mim. 123, *pl. 37.* 1819.
Cassia rotundifolia bauhiniæfolia Benth. in Mart. Fl. Bras. 15²: 162. 1870.

Type locality: Río Orinoco, near Carichana.
Tolima, *Lehmann 2373* (cited by Micheli as *Cassia rotundifolia* var. *grandiflora*), *8479, B.T.1057, B.T.1113.* Without locality, *Mutis 2343, 2353, 4282.*

11. **Chamæcrista pilosa** (L.) Greene, Pittonia 4: 28. 1899.

Cassia pilosa L. Syst. Nat. ed. 10, 1017. 1759.

Type locality : Not given.
Santa Marta, *H. H. Smith 276.* Sabanilla, Atlántico, *Pennell 12071.* Barranquilla, *Elias 398, 787.* Venezuela ; Trinidad ; Guatemala ; Jamaica ; Cuba.

12. **Chamæcrista serpens** (L.) Greene, Pittonia 4: 29. 1899.

Cassia serpens L. Syst. Nat. ed. 10, 1018. 1759.
Cassia prostrata H. & B. ; Willd. Enum. 441. 1809.

Type locality : Not given.
Santa Marta, *H. H. Smith, 67.* Sabanilla, Atlántico. *Pennell 12072.* Melgar, Cundinamarca, *Pennell 2886.* Medellin, *Archer 790, 835.* Dagua, El Valle, *Pennell 5661.* Venezuela to Brazil and Paraguay ; Guatemala ; Jamaica ; Cuba.

13. **Chamæcrista supplex** (Mart.) Britton & Rose.

Cassia supplex Mart. ; Benth. in Mart. Fl. Bras. 15 ²: 163. 1870.

Type locality : Pernambuco, Brazil.
Santa Marta, *H. H. Smith 66.* Brazil.

14. **Chamæcrista trichopoda** (Benth.) Britton & Rose.

Cassia trichopoda Benth. in Mart. Fl. Bras. 15 ²: 163. 1870.

Type locality : Brazil.
Santa Marta, *H. H. Smith 709.* Venezuela (according to Bentham) ; Bolivia and Brazil.

15. **Chamæcrista Pennellii** Britton & Rose, sp. nov.

Subherbacea, ramulis pilosis ; stipulæ linear-lanceolatæ. longe acuminatæ ; petioli pilosi, glandula sessile ; foliola 4–7-juga, valde multivenia, oblonga vel oblongo-oblanceolata, obtusa vel rotundata, supra glabra, longiciliata, subtus in costa sparse pilosa. costa excentrica ; bracteæ 2, lanceolatæ ; sepala lanceolata, sparse pilosa ; petala obovata ; stamina 10 ; legumen laxe pilosum.

Subherbaceous, low, about 2 dm. high or less, the twigs slender, pilose. Stipules linear-lanceolate, long-acuminate, 8 mm. long, sparingly long-ciliate : petioles 4–6 mm. long, pilose, the gland small, depressed, sessile ; rachis loosely pilose, subulate-tipped ; leaflets 4–7 pairs, strongly many-veined, oblong or oblong-oblanceolate, 5–10 mm. long, 2–3 mm. wide, glabrous and shining above, long-ciliate, sparingly pilose on the under side of the midvein, rounded or obtuse, abruptly subulate-tipped, the base subtruncate, the midvein excentric : peduncles slender, 2–3 cm. long, bearing 2 lanceolate bracts about 3 mm. long above the middle ; sepals lanceolate, acuminate, sparingly pilose, about 13 mm. long ; petals about 15 mm. long, obovate ; stamens 10 ; legume linear, about 5 cm. long and 4 mm. wide, loosely pilose.

Open loam between Fusagasugá and Pandi, Cundinamarca, Colombia, November 30, 1917, *Pennell 2749*, type (U.S.). Fusagasugá, *Tracey 397.*

16. **Chamæcrista flexuosa** (L.) Greene, Pittonia 4: 27. 1899.

Cassia flexuosa L. Sp. Pl. 379. 1753.
Cassia arenaria H. B. K. Nov. Gen. & Sp. 6: 370. 1824.

Type locality, Brazil.
Rincón Hondo, Magdalena, *Allen 206.* Venezuela to British Guiana, Bolivia and Brazil ; Panama to Oaxaca ; Cuba.

17. **Chamæcrista Browniana** Britton & Rose, N. Am. Flora 23: 293. 1930.

Type locality : Between Quetamé and Susumuco. Colombia.
Between Quetamé and Susumuco. Cundinamarca, *Pennell 1351* (type). Bolivia ; El Salvador.

18. **Chamæcrista simplex** Standley, Contr. U. S. Nat. Herb. **18**: 103. 1916.

Type locality : Near Chepo, Panama.
Frequent at middle altitudes in northern Columbia. Panama.

19. **Chamæcrista patellaria** (DC.) Greene, Pittonia **4**: 32. 1899.

Cassia patellaria DC.: Collad. Hist. Cass. 125. 1816.

Type locality : Cayenne.
Frequent in Colombia. Venezuela, Tobago and Trinidad to French Guiana, Bolivia and Brazil; Panama to Veracruz; Greater Antilles.

20. **Chamæcrista flavicoma** (H. B. K.) Greene, Pittonia **3**: 242. 1891.

Cassia flavicoma H. B. K. Nov. Gen. & Sp. **6** : 366. 1824.

Type locality : Orinoco River.
Frequent at middle altitudes in Colombia. Venezuela.

21. **Chamæcrista stenocarpa** (Vogel) Standley, Contr. U. S. Nat. Herb. **18**: 104. 1916.

Cassia stenocarpa Vogel. Syn. Cass. 68. 1837.

Type locality : Brazil.
Santa Marta, *H. H. Smith 275, 2537*. Turbaco, Bolívar, *Killip & Smith 14462; Heriberto 117*. Without locality. *Mutis 2370*. Ecuador; Venezuela; Brazil; Panama to Veracruz and Guerrero ; Jamaica ; Cuba ; Curaçao.

22. **Chamæcrista riparia** (H. B. K.) Britton, Bull. Torr. Club **44**: 11. 1917.

Cassia riparia H. B. K. Nov. Gen. & Sp. **6** : 369. 1824.

Type locality : Magdalena River, near Mompox, Colombia.
Since, Bolívar, *Pennell 4029*. Recorded by authors from a wide range in tropical America, but, apparently, restricted to northern Colombia.

23. **Chamæcrista Andreana** Britton & Killip, sp. nov.

Frutex; stipulæ lineari-lanceolatæ; petioli glandula scutellata, sessilis; foliola 3–5-juga, oblonga, chartacea, glabra, ciliolata, dense pennivenia, costa excentrica : sepala lanceolata, glabrata.

A shrub, the short slender twigs sparingly short-pubescent or glabrous. Stipules linear-lanceolate, long-acuminate. glabrous or sparingly ciliate, 4–6 mm. long; petiolar gland scutellate, orbicular, sessile, about 0.4 mm. broad; leaflets 3–5 pairs, oblong, chartaceous. glabrous, ciliolate, rounded or emarginate, mucronate. closely pinnately many-veined, the prominent midvein excentric : pedicels filiform, somewhat pubescent, 5–7 mm. long; sepals lanceolate, acuminate, nearly glabrous, 6–7 mm. long; larger petals about 1 cm. long.

Sandy soil, Piedras and Ibagué. eastern base of Mt. Quindío, Tolima. Colombia, March 3, 1876, *André 1974*, type (N.Y.), cited as *Cassia Chamæcrista* L. by Micheli.

24. **Chamæcrista arborescens** Britton & Killip, sp. nov.

Frutex pilosus ; stipulæ anguste triangulato-lanceolatæ; petioli glandula crassa, subclavata : foliola 9–13-juga, chartacea, oblonga vel (suprema) oblongo-oblanceolata, multinervia, ciliata, glabra, in costa subexcentrica sparse pilosa ; legumen lineare, sparse et breviter pubescens.

A shrub, 3–4 m. high, the branches rather stout, pilose, at least when young. Stipules narrowly triangular-lanceolate, pilose, long-acuminate, 10–12 mm. long, few-nerved : petioles short, bearing a stout subclavate gland about 1.5 mm. long; leaves 7–9 cm. long, the rachis pilose; leaflets 9–13 pairs, chartaceous, oblong (or the upper pair oblong-oblanceolate), rather strongly many-nerved, obtuse or acutish, mucronulate, ciliate, dull. glabrous and dark green above, paler green and sparingly pilose on the somewhat excentric midvein beneath;

fruiting pedicels stout, pilose, 1.5–2 cm. long, 2-bracteolate above the middle; legume linear, 4–5 cm. long, 8 mm. wide, tipped, sparingly short-pubescent.

Open hillside, Culagá Valley, near Tapatá, north of Toledo, Norte de Santander, Colombia, 1800–2000 m. altitude, March 4, 1927, *Killip & Smith 20146*, type (N.Y.).

Chamæcrista glandulosa (L.) Greene, recorded by Bentham from Colombia, is restricted in distribution to Jamaica.

Cassia gracilis Kunth, recorded by Bentham from Colombia, has its type locality near San Borja, on the Río Orinoco, Venezuela, and is not known to us from Colombia.

Chamæcrista mimosoides (L.) Greene, with the type locality in Ceylon, has been recorded by authors from a wide range in tropical America, but it appears to be restricted to tropical Asia.

31. GRIMALDIA Schrank, Bot. Zeit. Regensb. 4: 184. 1805.

Type species: *Grimaldia opeifera* Schrank.

KEY TO SPECIES OF GRIMALDIA

Leaflets obovate to orbicular, rounded or emarginate
   mucronate .... 1. *G. viscosa.*
Leaflets elliptic to ovate, acute, aristellate.......... 2. *G. colombiana.*

1. Grimaldia viscosa (H. B. K.) Britton & Rose.

Cassia viscosa H. B. K. Nov. Gen. & Sp. 6: 360. 1824.

Type locality: Mesa de Cuello, near Contreras, and Ibagué, Colombia.
Upper Lebrija Valley, Santander, *Killip & Smith 16264*. Villavicencio, Meta, *Apollinaire Marie*.

Specimens from Brazil and British Guiana, here referred by authors, are **Grimaldia cuneifolia** (Vogel) Britton & Rose (*Cassia cuneifolia* Vogel, Syn. Cass. 51. 1837). Micheli cites André's 867 as *Grimaldia hispidula* (Vahl) Britton & Rose (*Cassia hispidula* Vahl), a species with which *G. viscosa* may prove to be synonymous.

2. Grimaldia colombiana Britton & Rose, sp. nov.

Frutex ad 1 m. altus vel subherbacea, dense glanduloso-pubescens, viscosa; stipulæ lineares; foliola 2-juga, elliptica vel ovata, acuta, aristulata, supra glabra, subtus pubescentia, ciliata; sepala oblonga; petala obovata; stamina 10; legumen lineare, utroque angustatum.

A shrub, about 1 m. high, or lower, or subherbaceous, the twigs, petioles and inflorescence densely glandular-pubescent and viscid. Stipules linear, 1–2 mm. long; leaflets 2 pairs, elliptic to ovate, subchartaceous, 1–4 cm. long, acute, apiculate or aristellate, glabrous above, ciliate, pubescent beneath; racemes few-several-flowered; pedicels slender, 10–15 mm. long; sepals oblong, acutish, sparingly pubescent, about 12 mm. long; petals obovate, reticulate-veined, short-clawed, about 15 mm. long; stamens 10, the anthers 4–5 mm. long; legume linear, flat, loosely long-pubescent or at length glabrate, short-beaked, narrowed at both ends, 2.5–3 cm. long, 5–6 mm. wide.

Northern slope of Mesa de los Santos, Santander, Colombia, 1000–1500 m. altitude, December 15, 1926, *Killip & Smith 15419*, type (N.Y.). Huila, Neiva, *Rusby & Pennell 1185*. Melgar, Cundinamarca, *Pennell 2854*. Villavicencio, Meta, *Pennell 1643*. (?) Río San Jorge, El Cauca, *André 2922*, cited by Micheli as *Cassia hispidula*.

32. PARKINSONIA L. Sp. Pl. 375. 1753.

Type species: *Parkinsonia aculeata* L.

1. Parkinsonia aculeata L. Sp. Pl. 375. 1753.

Parkinsonia spinosa H. B. K. Nov. Gen. & Sp. 6: 335. 1824.

Type locality: Tropical America.
Frequent in northern Colombia at low elevations. Venezuela and Margarita to Surinam; Galápagos; Panama to Chihuahua and Sonora; West Indies; Florida to Texas. SAUCE, GUAJIRO, RETAMO, YABO.

33. DELONIX Raf. Fl. Tell. 2: 92. 1836.

Type species: *Poinciana regia* Bojer.

1. Delonix regia (Bojer) Raf. Fl. Tell. 2: 92. 1836.

Poinciana regia Bojer; Hook. Bot. Mag. 56: *pl. 2884.* 1829.

Type locality: Madagascar.
Turbaco, Bolívar, *Killip & Smith 14419.* Girardot, *Pérez 377.* Barranquilla, *Elias 242.* Widely planted, and naturalized in tropical and subtropical America. Native of Madagascar.

34. CERCIDIUM Tulasne, Arch. Mus. Paris 4: 133. 1844.

Type species: *Cercidium spinosum* Tulasne.

1. Cercidium præcox (R. & P.) Harms, Bot. Jahrb. 42: 91. 1908.

Cæsalpinia præcox R. & P.; Hook. & Arn. Bot. Misc. 3: 208. 1832.
Cercidium spinosum Tulasne, Arch. Mus. Paris 4: 134. 1844.
Rhetinophyllum viride Karst. Fl. Col. 2: 25, *pl. 113.* 1862.
Cercidium viride Karst. Bot. Jahrb. 8: 346. 1887.

Type locality: Peru.
Cúcuta, Norte de Santander, *Killip & Smith 21016.* Tucaraca, Goajira, *Dawe 502.* Ecuador to Peru and Argentina; Venezuela; Curaçao; Hispaniola. QUICA.

35. HÆMATOXYLON L. Sp. Pl. 384. 1753.

Type species: *Hæmatoxylon campcchianum* L.

1. Hæmatoxylon Brasiletto Karst. Fl. Col. 2: 27, *pl. 114.* 1862.

Type locality: Foot of the Andes, northern Colombia.
Santa Marta, *H. H. Smith 258; Killip & Smith 21094, 21106; Dawe 480.* Goajira, *Dawe 575.* Venezuela; Curaçao; Bonaire. HALA, PALO DE BRASIL, BRASILETO.

36. LIBIDIBIA Schl. Linnæa 5: 192. 1830.

Type species: *Poinciana coriaria* Jacq.

KEY TO SPECIES OF LIBIDIBIA

Legume twisted; leaflets linear.................... 1. *L. coriaria.*
Legume straight; leaflets oblong to elliptic or obovate.
    Leaflets 3–5 pairs, elliptic. or the upper pair
      obovate, sparingly black-dotted............. 2. *L. punctata.*
    Leaflets 7–9 pairs, oblong.
      Leaflets 5–10 mm. long.................... 3. *L. corymbosa.*
      Leaflets larger, up to 16 mm. long........... 4. *L. Ebano.*

1. Libidibia coriaria (Jacq.) Schl. Linnæa 5: 193. 1830.

Poinciana coriaria Jacq. Sel. Stirp. Am. 123. 1763.
Cæsalpinia coriaria Willd. Sp. Pl. 2: 532. 1799.

Type locality: Curaçao.
Frequent in Bolívar and Santa Marta. Venezuela; Curaçao; Aruba; Bonaire; Panama to Sinaloa; Jamaica; Hispaniola; Puerto Rico; St. Thomas to Montserrat. DIVIDIVI, BARANÓ, LIBIDIBI.

2. Libidibia punctata (Willd.) Britton; Britton & Wilson, Sci. Surv. Porto Rico & Virgin Ids. 5: 378. 1924.

Cæsalpinia punctata Willd. Enum. 445. 1809.
Poinciana punctata Poir. in Lam. Encycl. Suppl. 4: 449. 1816.
Cæsalpinia paucijuga Benth. in Hook. Ic. Pl. 20: *pl. 1977.* 1891.

Type locality: Brazil (perhaps in error).
Santa Marta, *Record 40.* Puerto Colombia, Atlántico, *Elias 1146.* Ponedera, Atlántico, *Dugand 454.* ?Goajira, *Dawe 593* (foliage only).

3. Libidibia corymbosa (Benth.) Britton & Killip.

Cæsalpinia corymbosa Benth. Pl. Hartw. 117. 1839.

Type locality: Near Guayaquil, Ecuador.
Santa Marta, *H. H. Smith 17.* Ecuador; Peru.

4. Libidibia Ebano (Karst.) Britton & Killip.

Cæsalpinia Ebano Karst. Fl. Col. 2: 57, *pl. 129.* 1862.

Type locality: Northern Colombia.
Santa Marta, *Record 6½.* Endemic. Perhaps not distinct from *L. corymbosa.* EBANO.

37. TARA Molina, Sagg. Chile, ed. 2, 153. 1810.

Type species. *Tara tinctoria* Molina

1. Tara spinosa (Molina) Britton & Rose, N. Am. Flora 23: 320. 1930.

Poinciana spinosa Molina, Sagg. Chile 158. 1782.
Cæsalpinia pectinata Cav. Descr. 467. 1802.
Tara tinctoria Molina, Sagg. Chile, ed. 2, 153. 1810.
Cæsalpinia spinosa Kuntze, Rev. Gen. 3²: 54. 1898.

Type locality: Lima, Peru.
Frequent in Colombia. Venezuela to Peru, Bolivia and Chile; Cuba. GUARANGO, DIVIDIVI.

38. BRASILETTIA (DC.) Kuntze, Rev. Gen. 164. 1891.

Type species: *Cæsalpinia brasiliensis* Sw., not L.

1. Brasilettia mollis (H. B. K.) Britton & Killip.

Coulteria mollis H. B. K. Nov. Gen. & Sp. 6: 330. 1824.
Cæsalpinia mollis Spreng. Syst. 4: Cur. Post. 169. 1827.
Cæsalpinia acutifolia Johnston, Proc. Am. Acad. 40: 686. 1905.
Peltophorum Suringari Urban, Symb. Ant. 5: 363. 1908.
Peltophorum acutifolium Johnston, Proc. Bost. Soc. Nat. Hist. 34: 221. 1909.

Type locality: Santa Marta, Colombia.
Santa Marta, *H. H. Smith 705; Record 53.* Atlántico, *Dugand 851.* Curaçao; Aruba; Venezuela.

39. POINCIANA L. Sp. Pl. 380. 1753.

Type species: *Poinciana pulcherrima* L.

1. Poinciana pulcherrima L. Sp. Pl. 380. 1753.

Cæsalpinia pulcherrima Sw. Obs. Bot. 166. 1791.

Type locality: India.
Frequent or common in Colombia. All tropical and sub-tropical regions. In America north to Florida and Bermuda. Much planted for ornament. ANGELITO CLAVELLINA. GUACAMAYA, FLOR DE ANGEL, FLORITO, FLOR DE PAVO.

40. CÆSALPINIA L. Sp. Pl. 380. 1753.

Type species: *Cæsalpinia brasiliensis* L.

1. Cæsalpinia Andreana Micheli, Journ. de Bot. 6: 193. 1892.

Cæsalpinia bicolor C. H. Wright, Kew Bull. 1896: 22. 1896.

Type locality: Rio San Jorge. Colombia.
Rio San Jorge, El Cauca. *Andrè 291;* (co-type).   Patía, Nariño. *Lehmann 779;*, *B.T.610, B.T.8?;*.   Rio Loro, Huila, *Lehmann 8659.*   Garzón, Huila, *White 11.*   Peru? PALO BRAZIL.

41. GUILANDINA L. Sp. Pl. 381. 1753.

Type species: *Guilandina Bonduc* L.

1. Guilandina crista (L.) Small, Fl. SE. U. S. 591. 1903.

Cæsalpinia crista L. Sp. Pl. 380. 1753.
Guilandina Bonduccella L. Sp. Pl. ed. 2, 545. 1762.

Type locality: Ceylon.
Frequent in coastal sands, northern Colombia. Nearly all tropical and subtropical seacoasts, in America north to Bermuda, Florida, Tamaulipas, and Sinaloa. MATU, ORILLA DEL MAR.

42. SCHIZOLOBIUM Vogel, Linnæa 11: 399. 1837.

Type species: *Schizolobium excelsum* Vogel.

1. Schizolobium Parahyba (Vell.) Blake, Contr. U. S. Nat. Herb. 20: 240. 1910.

Cassia Parahyba Vell. Fl. Flum. 168. 1790.
Schizolobium excelsum Vogel, Linnæa 11: 399. 1837.

Type locality: near Rio de Janeiro, Brazil.
El Humbo, Boyacá, *Lawrance 547.* Veracruz to Panama. Brazil.

43. SWARTZIA Schreb. Gen. 518. 1791.

[TOUNATEA Aubl. Pl. Guian. 1: 549. *pl. 213.* 1775.]

Type species: *Swartzia alata* Willd.

KEY TO SPECIES OF SWARTZIA

Leaflet only 1.................................... 1. *S. Mutisii.*
Leaflets 3 to several.
  Under surface of leaflets densely pubescent: leaflets
    13 or 15.................................... 2. *S. robiniæfolia.*
  Under surface of leaflets glabrous; leaflets not
    more than 9.
    Petals scarcely longer than the calyx; stamens not
      more than 25............................. 3. *S. arborescens.*
    Petals much exceeding the calyx; stamens very
      numerous.
      Calyx sparingly pilosulous or glabrous.
        Rachis of leaves wingless. the leaflets obtuse
          at base; calyx splitting into 2 segments. 4. *S. Trianæ.*
        Rachis of leaves winged, the leaflets acute at
          base; calyx splitting into 3 or 4 segments. 5. *S. crocea.*
      Calyx tomentose.
        Upper leaflets 15–20 cm. long: longer stamens
          2–4 .... 6. *S. macrophylla.*
        Leaflets not more than 10 cm. long: longer
          stamens about 8...................... 7. *S. magdalenæ.*

1. **Swartzia Mutisii** Britton & Killip, sp. nov.

Ramuli appresso-pubescentes; petioli anguste alati; folia 1-foliolata, foliolum ovato-ellipticum, obtuse acuminatum, basi cuneatum, subcoriaceum, glabrum; inflorescentia axillaris, 3–4-flora, pedicellis tenuissimis; legumen juvenile oblongum, utroque acutum.

Twigs short-appressed-pubescent. Leaves 1-foliolate: petioles stout, 5–7 mm. long, narrowly winged, the wings subulate at apex; leaflet ovate-elliptic, 7–12 cm. long, 3.5–6 cm. wide, obtusely acuminate at apex, cuneate at base, subcoriaceous, lustrous, glabrous, conspicuously reticulate-veined; inflorescence axillary, 3 or 4-flowered, the branches sparingly pilosulous, the pedicels glabrous, very slender, 1–2 cm. long; buds globose, about 5 mm. in diameter, glabrous; immature legume oblong, 1.5–2 cm. long, compressed, acute at both ends, finely puberulous, its beak slender, about 5 mm. long, its stipe 7–8 mm. long.

Colombia, 1760–1808, *Mutis 4620* (type), *4617, 83*.

2. **Swartzia robiniæfolia** Willd.; Vogel, Linnæa 11: 171. 1837.

Type locality: Radigas de Honda, Colombia.
Radigas de Honda, Tolima, *Humboldt & Bonpland 1704* (co-type). MULATO.

3. **Swartzia arborescens** (Aubl.) Pittier, Journ. Wash. Acad. Sci. 11: 157. 1921.

Possira arborescens Aubl. Pl. Guian. 2: 934, *pl. 355.* 1775.
Rittera triphylla Sw. Prodr. 82. 1788.
Swartzia triphylla Willd. Sp. Pl. 2: 1220. 1799.
Tounatea arborescens Britton, Bull. Torrey Club 16: 325. 1889.

Type locality: French Guiana.
Umbría, Putumayo, *Klug 1938.* Guianas and Amazon basin of Brazil and Peru.

4. **Swartzia Trianæ** Benth. in Mart. Fl. Bras. 15²: 39. 1870.

Tounatea Trianœ Taubert, Bot. Centralbl. 47: 392. 1891.

Type locality: Tocaima, Bogotá, Colombia.
Honda, Tolima, *Ariste Joseph A310, A748.* Tocaima, Cundinamarca, *Triana* (co-type); *Pérez 2413.* Mariquita, *Triana.* Villavicencio, Meta, *Apollinaire Marie.*

5. **Swartzia crocea** (Vell.) Benth. in Mart. Fl. Bras. 15²: 23. 1870.

Mimosa crocea Vell. Fl. Flumin. 9: *pl. 17.* 1827.
Tounatea crocea Taubert, Bot. Centralbl. 47: 390. 1891.

Type locality: Brazil.
Fundación, Santa Marta, *Purdie.* Villavicencio, Meta, *Apollinaire Marie.* Brazil and perhaps Peru.

A related species, *S. myrtifolia* J. E. Sm.. was erroneously reported from Colombia by Bentham on the basis of a Moritz collection from Venezuela.

6. **Swartzia macrophylla** Willd.; Vogel, Linnæa 11: 172. 1837.

Type locality: Nares, Colombia.
Nares, Boyacá, *Humboldt & Bonpland* (photograph of type); El Humbo, Boyacá, *Lawrance 495.*

8. **Swartzia magdalenæ** Britton & Killip, sp. nov.

Ramuli dense rufo-tomentosi; rachis quadrangulata, anguste marginata; foliola 7 vel 9, oblonga vel elliptico-oblonga, obtuse acuminata, subcoriacea, glabra; inflorescentia paniculata, dense rufo-tomentosa; calyx tomentosus, in segmenta 3 ovato-oblonga ruptus: petalum suborbiculatum; stamina longiora ca. 8, breviora numerosissima.

Twigs densely rufo-tomentose. Stipules lance-linear, about 12 mm. long; rachis quadrangular, 8–12 cm. long, narrowly margined, sparingly pilosulous;

leaflets 7 or 9, oblong, rarely elliptic-oblong, 6–9 cm. long, 2–3 cm. wide, obtusely acuminate at apex, subacute at base, subcoriaceous, glabrous, the principal secondary nerves nearly 1 cm. apart; inflorescence paniculate, densely rufo-tomentose, the flowers in dense clusters, the pedicels very short; calyx about 8 mm. long, tomentose, splitting into 3 ovate-oblong segments; petal suborbicular, about 3.5 cm. wide; stamens numerous, the longer and stouter ones about 8, 12–13 mm. long, the shorter ones very numerous, capillary, 8–9 mm. long; ovary glabrous.

Magdalena Valley. Colombia, *Triana 457*, type.

Swartzia grandiflora Willd. is recorded from Colombia by Micheli, on the basis of *André 1830*, from the Magdalena Valley.

ADDENDUM

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1a. **Inga polita** Killip, sp. nov.

Arbor glabra, petiolis inflorescentiaque sparse puberulis; petiolus alatus, glandula concava; foliola 1-juga, crassa, coriacea, ovata vel ovato-oblonga, caudato-acuminata; flores umbellati, pedicellis calycibusque subæqualibus; calyx tenuis, lobis acutis.

Tree up to 5 m. high, glabrous throughout except the petioles and inflorescence. Petiole 1.5–2 cm. long, winged, the wings 2–2.5 mm. wide, subrevolute, the gland sessile, concave, 1 mm. in diameter; leaflets 1-pair, thickcoriaceous, lustrous, ovate or ovate-oblong, 10–18 cm. long, 5–7.5 cm. wide, caudate-acuminate, narrowed at base, the nerves strongly impressed above; peduncles 5–10 mm. long, puberulent; bracts subulate, rigid, persistent; flowers in umbels, the pedicels subequal to the calyces, puberulent; calyx slender, about 4 mm. long, very sparingly puberulent, its lobes acute; corolla (in bud) 7–9 mm. long, its lobes puberulent.

Buenaventura, El Valle, Colombia, near sea level, August 10, 1884, *Lehmann 8824*, type (Kew), cited by Micheli as *I. panurensis* Benth.

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27. *Inga panamensis*. Among the specimens at Kew under this name there is no *Linden 366* from Colombia. There is, however, a specimen of *Fendler 866* from "Colonia Tovar," in Venezuela, and this may have been the plant Bentham had at hand. Schlim's 256, doubtfully referred to *I. panamensis* by Bentham, is rather *I. caracasana* Pittier.

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27a. **Inga caracasana** Pittier, Arb. & Arb. Legum. 107. 1929.

Type locality: Curucuti, between La Guaira and Caracas, Venezuela.
Ocaña, Norte de Santander, *Schlim 256*. Another specimen from Ocaña, *Kalbreyer 273*, is referred here with hesitation.

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4a. **Pithecellobium picramnioides** Standley, sp. nov.

Arbor 6–9-metralis, trunco 15–20 cm. diam.; folia magna, bipinnata, pinnis unijugis, ca. 30 cm. longis, petiolo 3 cm. longo, apice glandula parva onusto; rhachis pinnæ gracilis, subteres, foliolis 3–5-jugis, breviter petiolulatis, oblongis vel lanceolato-oblongis, 8–11 cm. longis, 3–4.5 cm. latis, breviter subabrupte acuminatis, acumine acuto, basi oblique obtusis vel subrotundatis, glabris, supra in sicco olivaceis, nervis subimpressis, costa ut nervis subtus prominentibus, nervis lateralibus utroque latere 5 vel 6, valde adscendentibus; flores spicati,

spicis e trunco nascentibus, 30–50 cm. longis, pendulis, gracilibus, remote multifloris, rhachi flexuosa, minute tomentulosa, bracteis minutis, triangularibus, acutis; calyx campanulatus, basi rotundatus, 1.7 mm. longus, minute dentatus, dense adpresso-pilosulus; corolla in alabastro 4 mm. longa. extus dense minute adpresso-pilosula.

El Humbo region, Boyacá, Colombia, in heavy forest overhanging a stream bank, altitude 750 m., March 29, 1933, *A. E. Lawrance 718,* type (Field Museum).

"The wood is very hard. Center of the main stem hollow and full of water. Heart of the main stem contains a ring of ebony-colored wood half an inch thick. Flowers white." The proposed species belongs to the subgenus *Zygia*,[8] a group of trees confined in habitat almost or wholly to stream banks. *P. picramnioides* is noteworthy particularly for its greatly elongate flower spikes, which arise from somewhat elevated, cushion-like areas on the trunk of the tree.

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3a. **Calliandra angustifolia** Spruce; Benth. Trans. Linn. Soc. 30: 539. 1875.

Type locality: Huallaga River, eastern Peru.
Mocoa. Caquetá, *Sprague.* Peru.

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5a. **Calliandra purpurea** (L.) Benth. Lond. Journ. Bot. 3: 104. 1844.

Mimosa purpurea L. Sp. Pl. 517. 1753.
Inga purpurea Willd. Sp. Pl. 4: 1021. 1806.
Inga obtusifolia H. & B.; Willd. Sp. Pl. 4: 1022. 1806.
Calliandra obtusifolia Karst. Fl. Col. 2: 41, *pl. 171.* 1862.
Anneslia purpurea Britton, Mem. Brooklyn Bot. Gard. 1: 50. 1918.

Type locality: Tropical America.
Río César, Magdalena, *Dawe 635.* Venezuela; Lesser Antilles.

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5. *Mimosa debilis.* In attributing this species to Colombia Bentham evidently had in mind a Venezuelan collection of Fendler's.

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8a. **CYNOMETRA** L. Sp. Pl. 382. 1753.

Type species: *Cynometra cauliflora* L.

1. **Cynometra Schottiana** Hochr. Bull. N. Y. Bot. Gard. 6: 275. 1910.

Type locality: Atrato and Truando rivers, Colombia.
Atrato and Truando rivers, El Choco, *Schott 7* (type). TREMENTINO.

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15. *Chamæfistula subcoriacea.* The following specimens at Kew are apparently referable to this species although the upper pair of leaflets are 9–14 cm. long and the lower pair 6–11 cm. long: Santa Marta, *Purdie;* Río de Oro, Norte de Santander, *Kalbreyer 695;* Ocaña, *Schlim 6.*

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2a. **Chamæcrista brevipes** (DC.) Greene, Pittonia 4: 31. 1899.

Cassia brevipes DC.; Collad. Hist. Cass. 119, *pl. 9.* 1816.

Type locality: Panama.
Llanos de Cumaral, Meta, *André 1190.* Venezuela; British Guiana; Panama, Costa Rica.

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[8] In the foregoing treatment this species evidently is nearest related to *Zygia Lehmannii,* which has racemes only 4.5 cm. long. In order that the name may conform to the nomenclature of the present paper the new combination Zygia picramnioides (Standley) Killip must be made.—E. P. K.

PARTIAL LIST OF EXSICCATÆ

The following list consists chiefly of important older collections, which have been widely distributed :—

ANDRÉ : 213 Entadopsis polystachya : 215 Chamæfistula oxyphylla ; 216, in part, Inga fredoniana ; 216, in part, Inga pseudofastuosa ; 271 Mimosa colombiana : 294 Calliandra flavida ; 355 Schnella stenoloba ; 364 Inga oblanceolata ; 451 Mimosa colombiana ; 697bis Chamæfistula undulata ; 996 Chamæcrista tristicula ; 1049 Schnella umbriana ; 1063 Brownea Ariza ; 1151bis Calliandra colombiana ; 1190 Chamæcrista brevipes ; 1379 Calliandra Pittieri ; 1398 Chamæcrista flavicoma ; 1400 Calliandra Pittieri ; 1446 Senegalia riparia ; 1479 Ditremexa hirsuta ; 1519 Calliandra Pittieri ; 1555 Calliandra glaberrima ; 1737bis Schnella vestita ; 1810 Amaria petiolata ; 1857 Pithecellobium subglobosum ; 1919 Chamæcrista serpens ; 1938 Schnella nitida ; 1939 Inga oblanceolata ; 1974 Chamæcrista Andreana ; 1980 Chamæcrista serpens ; 1981 Mimosa somnians ; 2562 Cassia grandis ; 2621 Punjuba Lehmannii? ; 2625 Punjuba Killipii? ; 2735 Calliandra carbonaria ; 2773 Senegalia popayana ; 2914 Cæsalpinia Andreana ; 2921 Mimosa Andreana ; 2922 Grimaldia colombiana ; 3570 Poponax Pennatula ; 3615 Inga densiflora ; B.T.373 Acaciella Holtonii ; K413 Mimosopsis quitensis.

DAWE : 47 Calliandra Purdiei ; 152 Albizzia carbonaria ; 220 Adipera tomentosa ; 268 Inga marginata ; 378 Tara spinosa ; 410 Schnella longipetala ; 420 Inga heterophylla : 433 Zygia longifolia ; 442 Schnella stenoloba ; 456 Bauhinia Kalbreyeri ; 466 Pithecellobium lanceolatum ; 467 Arthrosamanea pistaciæfolia ; 470 Calliandra glaberrima ; 475 Samanea Saman ; 480 Hæmatoxylon Brasiletto ; 482 Neltuma juliflora ; 495 Peltogyne pubescens ; 502 Cercidium praecox ; 503 Libidilia coriaria ; 504 Schnella columbiensis ; 511 Pithecellobium dulce ; 519 Isandrina emarginata ; 525 Poponax tortuosa ; 570 Calliandra marginata ; 575 Hæmatoxylon Brasiletto ; 583 Senegalia polyphylla ; 590 Pithecellobium hymenææfolium ; 592 Isandrina emarginata ; 593 Libidibia punctata ? ; 615 Mimosa Velloziana ; 635 Calliandra purpurea ; 815 Pithecellobium dulce ; 831 Chamæcrista flavicoma ; 888 Prioria copaifera.

KALBREYER : 273 Inga caracasana? ; 625 Inga marginata ; 695 Chamæfistula subcoriacea? ; 696 Chamæfistula fluviatilis ; 755 Acaciella Holtonii ; 837 Bauhinia emarginata ; 1256 Mimosa somnians ; 1774 Chamæfistula Toroana? ; 1802 Bauhinia Kalbreyeri.

KLUG : 1622 Chamæfistula gigantifolia ; 1651 Senegalia tomentella ; 1664 Mimosa polydactyla ; 1716 Calliandra carbonaria ; 1733 Schnella umbriana ; 1737 Inga olivacea ; 1751 Chamæfistula Klugii ; 1830 Bauhinia tarapotensis ; 1865 Klugiodendron umbrianum ; 1938 Swartzia arborescens.

LEHMANN : 646 Inga spectabilis ; 779 Inga Holtonii ; 829 Inga popayanensis ; 904 Inga sordida ; 924 Senegalia Lehmannii ; 935 Adipera tomentosa ; 2089 Calliandra carbonaria ; 2187 Mimosa floribunda ; 2268 Leucaena glauca ; 2373 Chamæcrista bauhiniæfolia ; 2505 Chamæcrista flavicoma ; 2577 Schnella vestita ; 2935 Pithecellobium dulce ; 3055 Inga marginata ; 3079 Mimosa floribunda ; 3286 Chamæfistula macrophylla ; 3413 Mimosa pudica ; 3824 Inga polita ; 4070 Calliandra carbonaria ; 4614 Cassia grandis ; 4643 Tamarindus indica ; 4767 Mimosa floribunda ; 5360 Chamæfistula Toroana? ; 5364 Ditremexa leptocarpa ; 5366 Parkinsonia aculeata ; 5367 Calliandra Pittieri ; 5368 Calliandra tetragona ; 5369 Acaciella Holtonii ; 5511 Ditremexa leptocarpa ; 5750 Inga Ursi ; 5751 Inga popayanensis ; 5752 Inga Holtonii ; 6110 Neptunia plena ; 6679 Chamæfistula macrophylla ; 7343 Chamæfistula speciosa ; 7792 Peiranisia velutina ; 7793 Chamæsenna pistaciæfolia ; 7794 Cæsalpinia Andreana ; 7808 Inga popayanensis ; 8478 Chamæfistula Toroana ; 8479 Chamæcrista bauhiniæfolia ; 8539 Chamæsenna pistaciæfolia ; 8623 Punjuba Lehmannii ; 8659 Cæsalpinia Andreana ; 8764 Tara spinosa ; 8986 Inga Ruiziana ; 8987 Pseudovouapa stenosiphon ; 8989 Zygia Lehmannii ; B.T.364 Punjuba Lehmanni ; B.T.372 Herpetica alata ; B.T.373 Acaciella Holtonii ; B.T.565 Calliandra carbonaria ; B.T.610 Cæsalpinia Andreana ; B.T.622 Inga cycladenia ; B.T.822 Peiranisia

velutina : B.T.824 Cæsalpinia Andreana ; B.T.827 Peiranisia velutina ; B.T.1057 Chamæcrista bauhiniæfolia ; B.T.1095 Chamæcrista Lehmannii ; B.T.1113 Chamæcrista bauhiniæfolia ; K96 Chamæcrista tristicula ; K842 Mimosa floribunda.

LINDEN : 696 Calliandra glomerulata ; 1336 Chamæfistula speciosa ; 1500 Mimosa floribunda ; 1501 Mimosa spiciflora ; 1517 Pithecellobium forfex.

SCHLIM : 2 Peiranisia santanderensis ; 6 Chamæfistula subcoriacea? ; 98 Calliandra tetragona ; 106 Chamæcrista patellaria ; 152 Inga punctata ; 172 Acaciella Holtonii ; 173 Mimosa polycarpa ; 174 Chamæcrista patellaria ; 203 Calliandra Purdiei ;204 Inga santanderensis ;256 Inga caracasana ;268 Emelista pilifera ; 269 Bauhinia ungulata ; 270 Schnella nigra ; 281 Chamæcrista Schlimii ; 517 Inga ingoides ; 939 Havardia platyloba ; 941 Isandrina emarginata ; 942 Mimosa oligacantha.

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Calliandra Pittieri Standley.   Near La Cumbre, in the Western Cordillera (*Pennell & Killip 5978*).

Chamœsenna velutina Britton & Killip, sp. nov. Mutiscua, in the Eastern Cordillera (type).

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MIMOSACEÆ AND CÆSALPINACEÆ OF COLOMBIA

(Synonyms in italics)

ANNALS

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YELLOWSTONE THERMAL MYXOPHYCEAE

BY

JOSEPH J. COPELAND

YELLOWSTONE THERMAL MYXOPHYCEAE *

By Joseph J. Copeland

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INTRODUCTION *

LOCATION AND NATURE OF THE YELLOWSTONE NATIONAL PARK

Yellowstone National Park, located in northwestern Wyoming and encroaching slightly upon Idaho and Montana, is a region of unparalleled richness in respect to hot springs, geysers, steam vents, and accompanying thermal phenomena. The Park is approximately sixty-two miles long by fifty-four miles wide, and thus has an area of about 3426 square miles. The Yellowstone is essentially a broad volcanic plateau, surrounded on the northwest, north, east, and south by mountain ranges rising two to six thousand feet above the central plateau. The plateau itself, with an average elevation of about eight thousand feet is rolling, hilly, or even semi-mountainous in part. The irregular contour is increased by deep valleys and gorges; among these the Yellowstone, Gibbon, Madison, and Gardiner canyons are notable.

On the north and northwest the Gallatin Range incloses the Park; on the northeast edge of the Park the Snowy Range, separated from the Gallatins by the Gardiner River Valley, continues the mountainous boundary; connected with the Snowy Range by a group of irregular, rugged mountains, the Absaroka Range extends along the eastern border; and to the south the Tetons almost complete the circle of mountains. In all these ranges there are extensive signs of previous igneous activity: intrusive dikes and sheets: along the northwest, stocks, laccolites, bathyliths, bysmaliths; and in the interior of the Park toward the northeast portion an extinct volcano. The central plateau is composed primarily of extrusive igneous rock: andesites, rhyolites, and basalts, lying probably on Mesozoic (Cretaceous) and Tertiary (Eocene and Miocene) deposits.

GEOLOGICAL HISTORY

The mountains surrounding the Park are thought to be of approximately the same age, and were elevated chiefly toward the close of the Cretaceous, although preliminary deformation and elevation took place in the Comanchean (Early Cretaceous). The geological stresses with

accompanying faulting and deformation continued well into the Tertiary.
However, during this period the chief activity seems to have been igneous
and eruptive. Enormous quantities of extrusive material were erupted,
and at the same time significant intrusions took place. This volcanic
activity, beginning as a major process during the Eocene, reached its
greatest extent in the Miocene, and slowed up decidedly by the opening
of the Pliocene. There has been no igneous activity in the Yellowstone
within historic times and the entire process may for the present be con-
sidered extinct. By the elevation of the mountains encircling the Yellow-
stone a basin of considerable extent was produced. The extrusions which
followed in the Tertiary so nearly filled this basin that there is, instead,
an elevated, rough plateau. The most important extrusive rock in the
Park is rhyolite. The beds of this felsitic rock are in places certainly
three thousand feet thick, and the plateau, with a size of approximately
fifty by forty miles, must include at least one thousand cubic miles of
this extrusive rhyolite, along with other volcanic rock.

While the surface of this mass has in general cooled thoroughly, the
deeper portions have retained a considerable amount of heat. This is
indisputably demonstrated by the numerous geysers, thermal springs,
steam vents, mud pots, fumaroles, and warm areas. At least four thou-
sand thermal springs (of various types) are present—averaging about one
to each square mile.

During the Pleistocene extensive glaciation took place, and with the
erosion that has continued since the final extrusions marked changes have
been produced in the topography. The many lakes (Yellowstone, Heart,
Lewis, Shoshone, etc.) and the numerous glaciated valleys are particularly
characteristic of the former, while the canyons and worn mountains are
largely due to the latter cause.

The greater part of the Yellowstone is forested, and in general, signs
of previous volcanism are well buried.

ALGOLOGICAL STUDIES IN THE YELLOWSTONE

The great abundance of Myxophyceae in the thermal springs has been
such a striking feature that all who have written of the Yellowstone
have mentioned or commented on it. Even the earliest accounts of the
Park described the brilliant vari-colored growth of gelatinous material
covering the wet rock, sides and bottoms of the spring pools, and the
slopes and runoffs of the geysers. A. M. Edwards (1872) described
rather briefly some of these growths and incrustations, especially in the
geyser basins. He gave no data on the algae present and believed part or
all of the algal growth was some bizarre form of silica. Up to almost

1890, the more frequently expressed view was that the majority of the material was non-living.

Walter W. Weed (1889a, 1889b, 1889c) has given accounts of the Yellowstone from several angles. Primarily a geologist, Weed was interested in the algae, especially in their relationship to deposition. His descriptions of the spring and geyser formations are quite full, and analyses of the waters, made under his direction, cast light on the ecology of the springs. He pointed out the important geological rôle of the algae, and recognized them as chiefly blue-greens. In the geyser basins, he remarked on the importance of *Calothrix gypsophila* (*Dichothrix gypsophila* (Kütz.) B. & F.) or its juvenile form *Mastigonema thermale* (*Calothrix thermalis* (Schw.) Hansg.) (!) in depositing sinter. He also mentioned specifically *Leptothrix* (*Hypheothrix*) *laminosa* (*Phormidium laminosum* (Ag.) Gom.). He considered the algal sheaths to be composed of silica. (Undoubtedly the sheaths of certain Myxophyceae contain some hydrated silica, but the quantity is usually very small, and does not affect the presence and absence or nature of the sheath or matrix. Incrustation and impregnation with silica are quite different from the sheaths actually being of silica). The abundance and variety of diatoms in the cooler waters, especially in the "diatom marshes," as described by him. have no particular bearing here. In a later paper (1891) he discussed more fully the geological work of algae and mosses, with some emphasis on the Yellowstone. Later he collected other algae, which were reported by Tilden.

Miss Josephine Tilden (1897, 1898) collected in the Yellowstone in 1896 and 1897. Additional data were given by her in the American Algae [Exsiccatae] over a period of several years; and still later (1910) she summarized the data on Yellowstone Myxophyceae and made certain changes in her records. The results of her work were not particularly satisfying. She reported several species of Myxophyceae, giving for them mostly definite localities and some data as to the temperature at which they occur. Some of her records are in need of confirmation and others of revision. Several of her observations are deserving of a detailed discussion. This will be undertaken with the several species later in the paper.

B. M. Davis (1898). after studying the thermal flora in the Yellowstone for a rather short period, clearly recognized the problems presented there. The majority of his observations were on the springs at Mammoth, although he was acquainted with the geyser basins and studied them as well. In making statements or drawing conclusions he was quite conservative and careful. As a result his paper was decidedly reliable as far as it went. He stated that 85° C. was not far from the upper limit of

life in the springs. At Mammoth, where corded white streamers growing in and around the vents of the springs are conspicuous, he showed that these are composed of living organisms, imbedded in a jelly, and surrounded with an abundant sulphur deposition. The organisms, rather variable in form, he thought possibly were Bacilli. He noted the growth of *Phormidium* at temperatures up to 75° C. At the Grand Prismatic Spring, Midway Basin, he noted *Spirulina* in quite hot water, and *Anabaena* in cooler water. He did not attempt to place specifically the algae studied. Some of his drawings could, with little chance for error, be referred to definite species.

Paul Richter (1898) described two new species of Myxophyceae from Yellowstone material: *Calothrix calida* and *Calothrix Kuntzei*—both from "geysers in Yellowstone." He stated that *C. calida* grew at a temperature of 62.5° C. The temperature, I believe, is higher than any species of *Calothrix* ever tolerates.

W. A. Setchell (1903) gave the results of a careful and accurate study of the thermal limits of algal growth and of life in the Yellowstone. His results are presented below:—

	Calcareous waters	Silicious waters
Living organisms	70-71° C.	89° C.
Blue-green algae	60-63° C.	75-77° C.

He noted the presence of "unicellular forms peculiar to thermal waters" in the hot springs, but did not elaborate on them. Practically no mention was made of the species present.

Prát (1929) described the new species *Plectonema yellowstonense,* from Mammoth, growing on *Chara,* in tepid water; *Oscillatoria Ulrichii,* from Mammoth; *Symploca Nemecii,* from Mammoth; and *Phormidium yellowstonense,* from Mammoth, the last three growing in a lime deposit of certain springs. He also noted the presence of *Polychlamydum calcicolum* Kuff. in certain springs of the same region.

The algae of hot springs in other parts of the world have been studied to a variable degree. In Europe and northern Africa the thermal Blue-greens have received the most attention and are reasonably well known. Those of Iceland have been studied by several algologists, including G. S. West and Boye Petersen. However, the Yellowstone contains more hot springs than all of Europe, Africa, and Iceland combined, and its thermal flora is unquestionably larger and more varied than that of all Europe and Africa.

The present study was begun in the summer of 1928, and has included field study from then until 1934. Extensive collections of material have

been made and are the basis for the taxonomic and morphological phases of the work. The majority of the collections are preserved in fluid; several species have been studied in pure cultures, and preliminary identification was carried on in the field. The field studies have been limited to the summer seasons. All determinations of acidity, temperature, and abund-
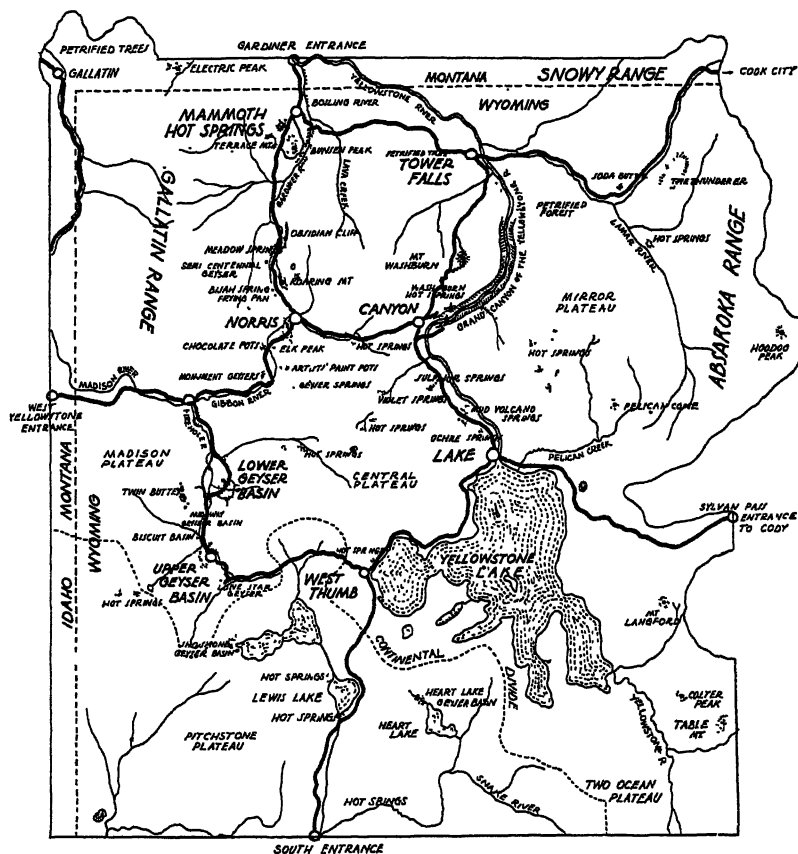
FIG. 1.—Map of the Yellowstone National Park, showing the location of the more important hot spring groups.

ance were made at the sites studied. Temperatures were recorded with thermometers tested both before use and at the end of the season, and are corrected to the nearest 0.1° C. The pH. determinations were made with the use of both electrometric and colorometric apparatus. Types of new species and varieties are deposited in the Herbarium of the New York Botanical Garden.

SURVEY OF THE YELLOWSTONE HOT SPRINGS

The greater portion of the important springs occur in a few large groups, of which the Mammoth Hot Springs, Lower Geyser Basin, Upper Geyser Basin, and Norris Geyser Basin are the largest, most spectacular and accessible. The last three mentioned are notable in including geysers —eruptive hot springs. The Mammoth Hot Springs are notable for the terraces they have built up. Less important spring groups and isolated springs are numerous. In the following list are included only those springs and thermal sites studied in the course of the present investigation. It will be noticed that the list is far short of including the four thousand odd springs in the Park. Where such data were recorded, the temperature and the acidity or alkalinity at the vent are given. In many cases it was physically impossible to determine such facts since the vent is inaccessible either because of its position or the high temperature of the water around it. In other cases the unavoidable damage to the spring formations in reaching the vents made it impractical and undesirable to obtain that information. Since conditions at the exact points where the algae were growing was of immediate interest, and the conditions at the vent of secondary interest, no systematic attempt was made to collect such information. In general, algae were taken for examination from several sites in each spring in order to determine their thermal range and to make certain that as nearly all species present as possible should be collected. This in some cases involved as many as forty collections from a single spring.

Mammoth Hot Springs (Elev. cir. 6.500 ft.)

Hymen Terrace	73.0° C.	pH. 6.50
Cleopatra Terrace	69.2° C.	pH. 6.55
Diana Terrace	67.4° C.	pH. 6.55
Minerva Terrace	68.3° C.	pH. 6.50
Jupiter Terrace	73.0° C.	pH. 6.45
Mound Terrace	71.0° C.	pH. 6.50
Main Terrace	69.8° C.	pH. 6.50
Blue Springs	73.0° C.	pH. 6.45
Canary Spring	74.0° C.	pH. 6.45
The Esplanade		pH. 6.55
Narrow Gauge Terrace	70.0° C.	pH. 6.55
Angel Terrace	72.5° C.	pH. 6.55
White Elephant Back	63.0° C.	pH. 6.60
White Elephant Grottoes. 1	49.0° C.	pH. 6.55
White Elephant Grottoes, 2	42.8° C.	pH. 6.75
Orange Spring Mound		
Orange Spring Mound, Jr.	60.0° C.	pH. 6.40

Stygian Caves .... 34.0° C....... pH. 7.10
Sunken Springs .... 52.0° C....... pH. 6.35
Soda Spring, at Mammoth (Elev. cir. 6,600 ft.)
   Soda Spring .... 30.0° C....... pH. 6.50
Boiling River Group (Elev. cir. 5,700 ft.)
   Boiling River .... 54.0° C....... pH. 6.60
   Riverside Cone .... 53.5° C....... pH. 6.60
   Boiling River Cave .... 30.2° C. ....
   Boiling River Cave Spring .... 53.4° C....... pH. 6.60
Meadow Springs Group, one half mile north of Roaring Mountain (Elev. cir.
   7,500 ft.)
   Sixteen unnamed springs:
      No. 1 .... 34.8° C....... pH. 7.80
      No. 2 .... 37.2° C....... pH. 6.20
      No. 3 .... 38.0° C....... pH. 7.60
      No. 4 .... 43.2° C....... pH. 7.55
      No. 5 .... 50.0° C....... pH. 8.40
      No. 6 .... 51.2° C....... pH. 6.60
      No. 7 .... 55.0° C....... pH. 6.60
      No. 8 .... 62.5° C....... pH. 5.40
      No. 9 .... 62.0° C....... pH. 6.70
      No. 10 .... 88.5° C....... pH. 8.10
      No. 11 .... 91.4° C....... pH. 7.30
      No. 12 .... 85.2° C....... pH. 7.40
      No. 13 .... 69.5° C....... pH. 6.60
      No. 14 .... 63.5° C....... pH. 6.95
      No. 15 .... 62.2° C....... pH. 5.40
      No. 16 .... 41.5° C....... pH. 5.30
Bijah Spring Group (Elev. cir. 7,500 ft.)
   Bijah Spring .... 78.5° C....... pH. 7.40
   Two unnamed springs:
      No. 1 .... 47.2° C....... pH. 6.10
      No. 2 ....
Semi-centennial Geyser Region (Elev. cir. 7,500 ft.)
   Semi-centennial Geyser .... 70.8° C....... pH. 4.50
   Obsidian Creek, 1 .... 37.5° C....... pH. 2.80
   Obsidian Creek, 2 .... 42.3° C....... pH. 3.10
Roaring Mountain (Elev. cir. 7,500-7,900 ft.)
   Four unnamed springs on slope of mountain:
      No. 1 .... 88.0° C....... pH. 4.45
      No. 2 .... 79.2° C....... pH. 4.65
      No. 3 ....
      No. 4 ....
   Roaring Mountain Pond .... 22.2° C....... pH. 4.50
   Lemonade Creek .... 26.1° C....... pH. 3.80
Frying Pan Group (Elev. cir. 7,400 ft.)
   Frying Pan ....
   Five small unnamed springs:
      No. 1 .... 71.7° C....... pH. 4.70

No. 2 ....

No. 3 .... 89.4° C....... pH. 5.20

No. 4 ....

No. 5 ....

Norris Junction (Elev. cir. 7,500 ft.)

    Unnamed spring .... 46.0° C....... pH. 6.30

Norris Geyser Basin (Elev. cir. 7,400 ft.)

    Arsenic Geyser .... 91.0° C....... pH. 3.80

    Apple Green Geyser .... 89.0° C....... pH. 4.55

    Iris Spring .... 74.0° C....... pH. 4.40

    Emerald Spring .... 81.0° C....... pH. 4.60

    Orpiment Spring ....

    Verma Spring ....

    Green Dragon Springs .... pH. 4.70

    Hydrophane Springs ....

    Seven unnamed springs:

        No. 1 .... 93.0° C................

        No. 2 .... 90.2° C................

        No. 3 .... 76.0° C....... pH. 7.20

        No. 4 .... 31.0° C.............

        No. 5 ....

        No. 6 ....

        No. 7 ....

Elk Park (Elev. cir. 7,500 ft.)

    Large "Unnamed Spring" .... 63.0° C....... pH. 8.15

    Small unnamed spring .... 59.0° C....... pH. 8.15

Chocolate Pots (Elev. cir. 7,400 ft.)

    Five individually unnamed springs:

        No. 1 .... 56.6° C....... pH. 6.20

        No. 2 .... 55.2° C....... pH. 6.60

        No. 3 ....

        No. 4 ....

        No. 5 ....

Artist's Paintpots (Elev. cir. 7,500 ft.)

    Swimming Pool Spring .... 37.3° C....... pH. 8.40

    Orange Paintpot .... 93.8° C.............

    Sinter Gravel Seep .... 39.4° C.............

    Eleven unnamed springs:

        No. 1 .... 50.0° C....... pH. 7.95

        No. 2 .... 63.8° C....... pH. 8.30

        No. 3 .... 91.1° C....... pH. 8.35

        No. 4 .... 90.0° C.............

        No. 5 ....

        No. 6 ....

        No. 7 ....

        No. 8 ....

        No. 9 ....

        No. 10 ....

        No. 11 ....

Monument Geyser Basin (Elev. cir. 7,900 ft.)
    Monument Geyser .... 84.0° C....... pH. 8.00
    Sulphur Spring .... 90.0° C....... pH. 5.30
    Brimstone Pool .... 81.0° C....... pH. 4.60
    Bacon Fumarole .... 114.0° C..............
    Two unnamed springs:
        No. 1, alum seep .... 29.0° C....... pH. 3.00
        No. 2 ....
Gibbon Canyon Springs (Elev. cir. 6,900 ft.)
    Beryl Spring .... 92.0°C..............
Madison Junction Region (Elev. cir. 6,800 ft.)
    Terrace Spring ....
Twin Buttes Region (Elev. cir. 7,400 ft.)
    Imperial Geyser Crater Spring................. 89.0° C....... pH. 8.80
    Seep in Imperial Geyser Crater................ 45.6° C....... pH. 8.40
    Fumaroles near Imperial Geyser................ 104.0° C..............
    Mudpots near Imperial Geyser.................. 93.0° C..............
    Spray Geyser .... 65.0° C....... pH. 8.80
    Fairy Creek Spring............................ 43.0° C..............
    Service Road Spring........................... 63.2° C....... pH. 8.30
Lower Geyser Basin (Elev. cir. 7,200 ft.)
    Ojo Caliente Spring ....
    Boulder Spring ....
    Fountain Geyser .... 92.0° C..............
    Firehole Lake................................. 36.1° C....... pH. 8.30
    Black Warrior Springs...
    Hot Lake ....
    Pink Cone Geyser.............................. 90.0° C..............
    Great Fountain Geyser......................... 96.0° C..............
    Surprise Pool .... 93.1° C..............
    Five Sisters Springs.......................... 89.9° C....... pH. 8.20
    White Dome Geyser...................................... pH. 8.40
Midway Geyser Basin (Elev. cir. 7,200 ft.)
    Grand Prismatic Spring........................ 74.0° C....... pH. 8.10
    Opal Pool .... pH. 8.20
    Turquoise Pool................................ pH. 8.10
    Excelsior Geyser Crater....................... 90.0° C....... pH. 8.30
    Iris Pools..
    Tromp Spring.................................. 31.0° C..............
Biscuit Basin (Elev. cir. 7,300 ft.)
    Jewel Geyser .... 92.6° C....... pH. 8.45
    Black Pearl Geyser............................ 54.0° C....... pH. 8.55
    Silver Globe Spring .... 89.0° C..............
    Artemesia Geyser .... 86.0° C....... pH. 5.20
    Firehole River at entrance of spring overflow.... 35.9° C....... pH. 8.75
    Sapphire Pool................................. 93.0° C....... pH. 8.95
Upper Geyser Basin (Elev. cir. 7,300 ft.)
    Iron Springs..
    Morning Glory Pool .... 78.0° C..............

Riverside Geyser .... 94.0° C ....
White Pyramid Geyser Cone...
Punch Bowl Spring............................ 94.4° C .... pH. 9.15
Black Sand Pool .... 93.0° C .... pH. 8.95
Sunset Lake ....
Rainbow Pool..
Handkerchief Pool .... 56.5° C .... pH. 8.65
Emerald Pool .... 69.7° C .... pH. 8.95
Green Spring .... pH. 8.70
Castle Geyser...
Bijou Geyser .... pH. 8.95
Mastiff and Catfish Geysers.................................. pH. 8.95
Giant Geyser.................................. 94.0° C ....
White Pyramid Geyser Cone Seep............... 48.5° C .... pH. 8.80
Oblong Geyser................................. 93.0° C ....
Purple Pool..... ....
Goggles Spring Pool.......................... 44.2° C .... pH. 8.70
Chromatic Pool .... pH. 8.95
Beauty Pool...
Wave Spring................................... 49.0° C .... pH. 8.20
Grand Geyser..
Beach Spring .... 89.4° C ....
Lion Geyser.................................. 94.0° C ....
Old Faithful Geyser.......................... 93.6° C ....
Seventeen unnamed springs:

    No. 1 .... 69.8° C ...... pH. 8.65
    No. 2 .... 44.6° C ...... pH. 8.80
    No. 3 .... 48.3° C ...... pH. 9.00
    No. 4 .... 31.4° C ...... pH. 8.65
    No. 5 .... 37.0° C ...... pH. 9.00
    No. 6 .... 67.9° C ...... pH. 8.35
    No. 7 .... 88.8° C ...... pH. 8.35
    No. 8 .... 60.1° C ...... pH. 8.45
    No. 9 .... 55.0° C ...... pH. 8.90
    No. 10 .... 37.2° C ...... pH. 8.85
    No. 11 .... 85.7° C ...... pH. 8.25
    No. 12 .... 93.0° C ...... pH. 8.50
    No. 13 .... 84.2° C ...... pH. 9.00
    No. 14 .... 43.8° C ...... pH. 9.05
    No. 15 .... 28.1° C ...... pH. 8.85
    No. 16 .... 26.5° C ...... pH. 8.90
    No. 17 .... 90.7° C ...... pH. 8.90

Lone Star Region (Elev. cir. 7,700 ft.)
    Lone Star Geyser ....

Shoshone Geyser Basin (Elev. cir. 7.750 ft.)
    Eight unnamed springs:
        No. 1 .... 73.2° C ...... pH. 7.60
        No. 2 .... 87.7° C ...... pH. 8.00
        No. 3 .... 34.5° C ...... pH. 7.55

    No. 4 .... 62.4° C....... pH. 8.05
    No. 5 ....
    No. 6 ....
    No. 7 ....
    No. 8 ....
West Thumb (Elev. cir. 7,750 ft.)
    Fishing Cone...
    Sinter Cliff Seep..
    Paintpots .... 95.1° C............
    Five unnamed springs:
        No. 1 .... 67.0° C............
        No. 2 ....
        No. 3 ....
        No. 4 ....
        No. 5 ....
Crater Hills (Elev. cir. 7,750 ft.)
    Great Sulphur Springs........................ 91.0° C....... pH. 4.65
    Eleven unnamed fumaroles and springs:
        No. 1 .... 80.0° C....... pH. 4.60
        No. 2 .... 39.0° C....... pH. 4.50
        No. 3 ....
        No. 4 ....
        No. 5 ....
        No. 6 ....
        No. 7 ....
        No. 8 ....
        No. 9 ....
        No. 10 ....
        No. 11 ....
Mud Volcano Group (Elev. cir. 7,750 ft.)
    Dragon's Mouth Spring........................ 73.0° C............
    Mud Volcano.................................. 86.0° C............
    Eight unnamed springs and pots:
        No. 1 .... 50.6° C....... pH. 5.05
        No. 2 .... 67.0° C....... pH. 5.00
        No. 3 ....
        No. 4 ....
        No. 5 ....
        No. 6 ....
        No. 7 ....
        No. 8 ....
Ochre Spring Group (Elev. cir. 7,980 ft.)
    Ochre Spring................................. 36.0° C....... pH. 6.00
Canyon Group (Elev. cir. 7,100 ft.)
    Three unnamed springs in Yellowstone Canyon:
        No. 1 ....
        No. 2 ....
        No. 3 ....

Lewis Lake Region (Elev. cir. 7,750 ft.)
    Five unnamed springs:
        No. 1 ....
        No. 2 ....
        No. 3 .. ..
        No. 4 ....
        No. 5 ....
Several miscellaneous and mostly unimportant springs.
        Total... over 220 springs.

The temperatures found in the springs should be interpreted by comparison with the boiling point of water at the elevation of the springs (between 6,000 and 8,000 ft.), rather than with 100°C. The boiling points of water at various altitudes are listed below.

        6,000 ft.................................... 93.5° C.
        6,400 ft.................................... 93.0° C.
        6,800 ft.................................... 92.5° C.
        7,200 ft.................................... 92.0° C.
        7,600 ft.................................... 91.5° C.
        8,000 ft.................................... 91.0° C.

Of the springs not included in this study, those of the Heart Lake region, and the groups around the southern slopes of Mt. Washburn probably are the most important.

The source of water supplying the thermal springs is thought to be largely meteoric. This water, after penetrating mostly to no great depth, is heated by gases rising from the underlying rock, which is hot and has retained a part of its former mineralizing substances. The water is charged with any gases that are brought in contact with it and with any substances encountered on the way to the surface. Consequently, depending on the substratal nature, the springs vary greatly in their chemical composition.

DESCRIPTIVE LIST AND KEYS

MYXOPHYCEAE Wallroth

Fl. crypt. German., IV, 1833 (Myxophykea).
Stitzenberger in Rabenhorst's Algen Sachsens, 1860.

Syn.: Gloeosipheae Kützing, Phyc. gen., 1843.
    Cryptophyceae Thuret in LeJolis' Liste Alg. Cherbourg, 1863.
    Phycochromophyceae Rabenhorst, Fl. Europ. Alg., II, 1865.
    Cyanophyceae Sachs, Lehrbuch der Botanik, 4th ed., 1874.
    Schizophyceae Cohn, Jahrbuch. Ges. f. vaterl. Cultur, 1879.

Unicellular, colonial or multicellular algae, of variable color and appearance. Protoplast without differentiation into nucleus and cytoplasm, without chro-

matophores; with differentiation into outer pigmented chromatoplasm, and inner colorless central body. Vacuoles rare; pseudovacuoles present in mostly planktonic forms. Pigments chlorophyll, phycocyanin, phycoerythrin, and sometimes others; color of protoplast: blue-green, olive-green, golden, or less often rose, violet, golden-green or yellow-brown. Cell wall occasionally thin (without sheath or matrix) but usually gelatinized in outer portions (with a sheath or matrix) and very thick, colorless or golden, brown, yellowish, or sometimes reddish, blue, or violet. Motility often possessed by the thin-walled filamentous types, of a gliding or rarely undulant nature; mechanism of movement not understood, visible flagella or protoplasmic extrusions absent; planococci often produced by thick walled (integumented) species; non-filamentous colonies rarely motile. Food storage product glycogen or glycogen compounded with some protein; starch absent. Nutrition usually holophytic; less often saprophytic, parasitic, sapropeltic, or prototrophic. Cell division direct, either binary or rarely by multiple sporulation, or unequal with the formation of cells of unlike size; the new wall pinching in from the periphery of the cell. Fission usually transverse to the polar axis, rarely longitudinal. Multiplication through simple fission, exospores, endospores, nannocysts, planococci, gonidia (resting cells), rarely heterocysts, or usually through fragmentation of the plant body into definite (hormogonia) or indefinitely formed portions or into single cells. Encystment occurs in the hormocysts (many celled, heavily sheathed "hormogonia"), in the resting cells (the so-called "spores" or "gonidia," etc.) or in apparently unmodified filaments or cells. Sexual processes absent. Habitats varied, including: fresh water, planktonic or benthonic, attached or free; damp soil, rocks, bark, and the like; salt water, mostly in the intertidal zone, or at the surface and often planktonic; brackish water; supersaline water and marshes; hot and warm springs; sulphur springs; frequently symbiotic, in certain lichens, green algae, fungi, liverworts, water ferns, cycads, flowering plants; often attached to various plants and animals. Distribution cosmopolitan, with many cosmopolitan species.

The Myxophyceae on the whole are quite sharply separated from all other organisms. In cellular structure they are far simpler than the other algae. Nevertheless, there are certain other groups with which, in some cases, there is considerable difficulty in drawing a sharp line of separation. The close or overlapping groups are the Bangiales, Cyanochloridineae, Spirochaetales and the groups of Sulphur and Purple Bacteria. In the Yellowstone the first two present no problems; the Spirochaetes and the more or less independent Bacteria are in a few instances quite close to certain blue-greens.

The two organisms described by Lagerheim (1892) from Quito, Ecuador, as *Glaucospira agilissima* and *G. tenuior* combine characters of the Myxophyceae and of the Spirochaetales. They have a Spirochaete-like locomotion and the flexible membrane characteristic of the same group; on the other side they are blue-green in color and are photosynthetic. As

far as is known, their protoplasts might be moderately typical of either group. Concerning them Geitler (1925) states: "Vielleicht handelt es sich gar nicht um Cyanophyceen," but at the same time he follows Kirchner in including them in *Spirulina* Turp. In the Yellowstone I have found a species that is quite close to, but distinct from, those of Lagerheim. I am reviving the genus *Glaucospira* and placing the species in it. At the same time it would be recognized that, although similar in superficial appearance to *Spirulina,* the two genera are not at all close. Except for the rigid distinction between Algae, and Fungi plus Bacteria, *Glaucospira* might be placed in the Spirochaetales.

The distinction between the Sulphur Bacteria, Purple Bacteria, and Myxophyceae is in part none too clear. The rose-colored "blue-greens" and the purple to rose-colored holophytic or partially holophytic Bacteria are separated by poorly defined features. Certain of the filamentous blue-greens are practically devoid of chlorophyll and approach closely such genera as *Thiothrix* Winogr. I have attempted to follow as closely as possible the conventions in placing such forms.

The thermal and semi-thermal Yellowstone representatives of the Myxophyceae are numerous and include members of all three orders and of all the important families. In all, fourteen families and fifty-two genera have been found there. This constitutes the largest assemblage of genera of the group ever reported from any area of comparable size on the earth, and at the same time does not include many species that inhabit waters of low or normal temperatures. Undoubtedly if the non-thermal habitats of the same region were carefully studied, many or at least several others would be added. Among these genera that are to be expected there are such common ones as: *Merismopedia, Amphithrix, Petalonema, Aphanizomenon, Nostochopsis,* and *Homoeothrix.* It is notable that the Yellowstone springs house several genera not known elsewhere in North America. The large number of endemic species has necessitated the description of a number of new forms.

The taxonomic handling of the Myxophyceae in the preparation of this paper has been greatly accelerated by the very useful manuals written by Dr. Lothar Geitler (1925, 1930-32).

<div align="center">KEY TO THE ORDERS</div>

I. Intercellular protoplasmic strands (plasmodesma) absent; heterocysts absent; plants unicellular or colonial, rarely filamentous.
  1. Endospores and exospores absent; resting cells, nannocysts and planococci often present; cells without base-apical differentiation, or with such and united into free spherical colonies............CHROOCOCCALES (p. 19)

2. Endospores or exospores present; cells and colonies often attached and with base-apical differentiation..............CHAMAESIPHONALES (p. 68)

II. Intercellular protoplasmic strands (plasmodesma) present; plants filamentous; heterocysts present or absent; resting cells frequent...........
OSCILLATORIALES (p. 78)

CHROOCOCCALES Wettstein

Handbuch der syst. Botanik, 3rd ed., 1924

KEY TO THE FAMILIES

I. Plants unicellular or colonial, cells never united into filaments or pseudo-filamentous cell rows...........................CHROOCOCCACEAE (p. 19)

II. Cells arranged in pseudo-filamentous rows or in filaments, or cells in tips of gelatinous strands........................ENTOPHYSALIDACEAE (p. 64)

CHROOCOCCACEAE Naegeli

emend. Geitler, Synopt. Darst. Cyan., Beih. Bot. Centralbl, pt. 2, p. 41, 1925.

KEY TO THE YELLOWSTONE GENERA

1. Cells spherical, ovoid, or cylindrical with rounded ends.
　1. Ample tegument present, often not easily seen without staining.
　　A. Cells of the colony few, or many, and without regular orientation.
　　　a. Colony not becoming transformed completely into resting cells at maturity; no definite special outer membrane to colony.
　　　　ᐟ. Cells not individually encapsulated: matrix homogeneous.
　　　　　ǃ. Cells closely arranged.　　　　　　MICROCYSTIS (p. 20)
　　　　　ǃǃ. Cells loosely arranged.
　　　　　　♯. Cells spherical.　　　　　　APHANOCAPSA (p. 21)
　　　　　　♯♯. Cells elongate.
　　　　　　　x. Colonies of many cells.　APHANOTHECE (p. 24)
　　　　　　　xx. Colonies few-celled.　　RHABDODERMA (p. 44)
　　　　ᐟ*. Cells individually encapsulated, matrix more or less differentiated.
　　　　　ǃ. Cells spherical.
　　　　　　♯. Tegument loose, cells soon becoming spherical after fission.　　　　　　GLOEOCAPSA (p. 29)
　　　　　　♯♯. Tegument close, cells remaining flattened on adjacent faces.　　　　　　CHROOCOCCUS (p. 36)
　　　　　ǃǃ. Cells elongate.
　　　　　　♯. Matrix mostly homogeneous, not concentrically lamellate.
　　　　　　　　　　　APHANOTHECE (p. 24)
　　　　　　♯♯. Matrix mostly lamellate, often very obscurely so.
　　　　　　　　　　　GLOEOTHECE (p. 26)
　　　b. Colony becoming transformed completely into resting cells at maturity; definite special outer membrane around colony.
　　　　　　　　　　　ANACYSTIS (p. 46)
　　B. Cells of the colony numerous and arranged around the periphery of
　　　　　　　　　　　COELOSPHAERIUM (p. 45)

2. Tegument none or very thin and invisible.
    A. Cells spherical.   SYNECHOCYSTIS (p. 47)
    B. Cells elongate.   SYNECHOCOCCUS (p. 49)
II. Cells spindle-shaped, tapering at one or both ends.
                                        DACTYLOCOCCOPSIS (p. 63)

MICROCYSTIS Kützing

Linnaea, VIII, p. 372, 1833.

Syn.: *Anacystis* Meneghini, Consp. alg. Eugen., 1837, pro par.
     Polycystis Kützing
     Clathrocystis Henfrey, Mic. Journ., LIII, 1856.

Colonies spherical to elongate, often lobed and irregular, and at maturity often clathrate or broken.   Cells spherical to elongate, densely packed, usually without definite arrangement (in *M. merismopedioides* Fritsch in three dimensional rows), enclosed in a mostly homogeneous matrix.   Cell contents often with pseudovacuoles.   Cell division in one to three planes.
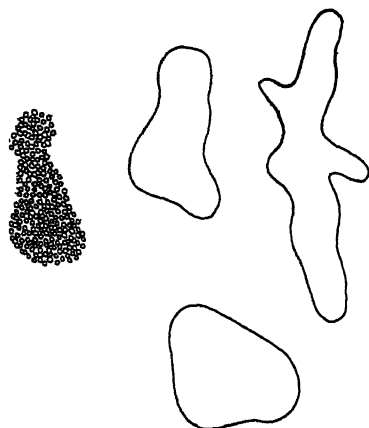
Fig. 2.—*Microcystis protea* (×500).

The majority of the species of *Microcystis* are planktonic, and several form water-blooms; a few are attached or benthonic.   They occur in fresh water, less often in brackish and salt water, and infrequently on damp soil.   Certain species are sapropeltic.   There have been no previous records of *Microcystis* from thermal sources.

A single Yellowstone species.

1. Microcystis protea, sp. nov.

Plants mixed with other algae, especially gelatinous Myxophyceae.   Colonies formless, lobed and irregular or occasionally, when small, almost spherical,

margin often indefinite, up to 200μ in greatest dimension, but mostly under 50μ. Cells spherical, without order, crowded (less so in small colonies), pale blue-green, 1.0-1.3μ in diameter, average distance between cells ¾ cell diameter. Cell contents homogeneous; pseudovacuoles absent. Matrix homogeneous, hyaline, almost invisible.

M. protea is close to *M. parasitica* Kütz. From it *M. protea* differs in having smaller cells, a less regular form, and by growing endophytically in masses of algae rather than epiphytically.

The commonest habitat for *M. protea* is among species of *Phormidium* and of *Oscillatoria,* either well buried or, when in the shade, near the surface. It has been found only in the Mammoth Hot Springs at temperatures of 31°–44° C., and at acidities of pH. 6.9–7.85. It has been found to be constantly rare, and is known from but few springs: White Elephant Grottoes (type: OS35), Stygian Caves, Angel Terrace, and Diana Terrace.

APHANOCAPSA Naegeli

Gattungen einzelliger Algen, p. 51, 1849.

Cells spherical or subspherical, united into formless, or less often, spherical to hemispherical soft gelatinous colonies or indefinite masses, often of considerable size or extent. Matrix gelatinous, mostly homogeneous and mostly hyaline, often with the individual sheaths somewhat incompletely confluent and indistinct but visible. Cell contents usually without pseudovacuoles. Cell division in three planes.

The species of *Aphanocapsa* live on damp soil and rocks, in fresh, brackish, and salt water, either planktonic or attached. A few species are endophytic in the matrix or strata of other Myxophyceae; a few are endolithic. A single species, *A. thermalis* Brügg, has been reported from thermal waters.

KEY TO THE YELLOWSTONE SPECIES

I. Cells 0.6-0.8μ in diameter, blue-green. *A. Tolliana* 1.
II. Cells 1.8-2.1μ in diameter, pinkish. *A. botryoides* 2.

1. Aphanocapsa Tolliana, sp. nov.

Colonies microscopically small, formless, spreading, often confluent, very pale blue-green, and often almost colorless; in slime of other algae. Single colonies up to 30 or 40μ in their greatest diameter, masses up to 400μ or more. Cells rather loosely arranged in a homogeneous, hyaline, almost invisible matrix, separated on an average by more than two diameters; cells spherical, 0.6-0.8μ in diameter, pale blue-green.

A. Tolliana is close to *A. delicatissima* W. et G. S. West. From it *A. Tolliana* differs in having a much less definite form, in having slightly

larger cells, a constantly hyaline and for the most part difficultly visible matrix, and in growing attached rather than planktonic. The two species are very readily separated.

While never abundant, *A. Tolliana* is found in most of the Mammoth Hot Springs. It has been recorded from Orange Spring Mound, Jr. (type: no. 77), Orange Spring Mound, White Elephant Grottoes, Angel Terrace, Jupiter Terrace, Minerva Terrace, Diana Terrace, Main Terrace,
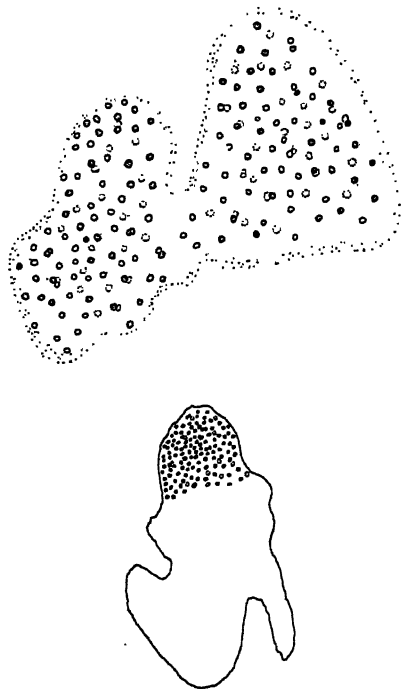
Fig. 3.—*Aphanocapsa Tolliana*, upper, small colony ($\times$1000); lower, large colony ($\times$500).

Mound Terrace, The Esplanade, Narrow Gauge Terrace, and Hymen Terrace. It has been found in water at temperatures from 31°–59° C., at acidities from pH. 6.45 to pH. 7.0. In most of the collections in which it was found, it was occasional to rare, growing usually with *Phormidium laminosum* (Ag.) Gom., *Phormidium purpurascens* var. *laminatum* (of this paper), and *Spirulina labyrinthiformis* Menegh., along with other incidental forms. The type was at 58° C. and pH. 6.7. The species is able to live well within the limits of truly thermal conditions.

2. Aphanocapsa botryoides, sp. nov.

Stratum extended, formless, attached to rocks in shallow water, gelatinous and often firm and membranous, salmon-red to pink in color, made up of numerous, incompletely confluent, minute colonies. Colonies spherical to formless, united into botryoidal clusters, often inclosing lime crystals, individual colonies up to 35μ in diameter. Matrix hyaline, homogeneous, often difficultly visible. Cells spherical to very short-ellipsoidal before division, close to moderately loose in position, without definite orientation, pink to pinkish green in color (blue-green in formalin preserved material), 1.8 to 2.1μ in diameter. Cell contents finely granular, without pseudovacuoles.
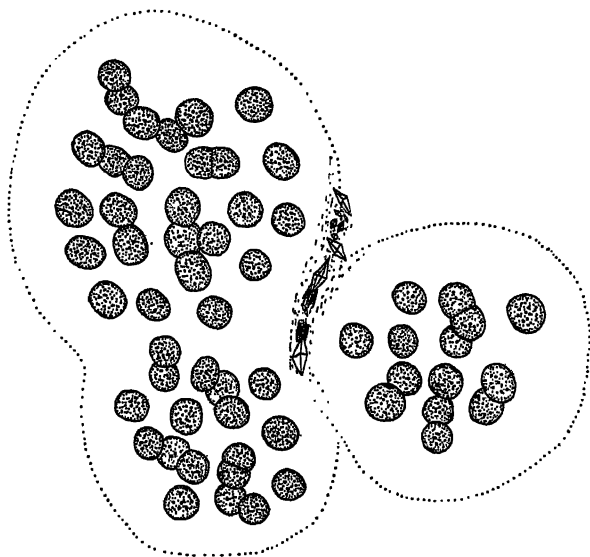
FIG. 4—*Aphanocapsa botryoides,* cluster of three colonies, inclosing lime crystals (×2400).

This species is quite distinct from all other members of the genus. The pinkish color is unique in the genus, and *A. botryoides* may be easily distinguished on morphological bases as well.

The alga has been found in a single site only. This situation, a small pool in the White Elephant Grottoes, Mammoth Hot Springs, is in moderate shade. The stratum of the plant covered the entire bottom of the pool; in part the growth was almost pure, in part it was mixed with other Myxophyceae, especially *Spirulina labyrinthiformis* Menegh. The type (no. 98) was at 42.8° C. and pH. 6.75; the extremes encountered by the alga in the pool were 39° C. and 54° C.; the acidity was almost constant.

APHANOTHECE Naegeli

Gattungen einzelliger Algen, pp. 59-60, 1849.

Cells elliptical to cylindrical with rounded ends, straight or curved, united in large numbers into formless or spherical to hemispherical soft gelatinous colonies or indefinite masses, often of considerable extent or size. Matrix gelatinous, homogeneous or with individual sheaths distinct or partially confluent, individual sheaths sometimes lamellate, hyaline to yellowish brown, rose, or violet. Cell contents usually without pseudovacuoles. Cell division always at right angles to the long axis of the cell.

The species of the genus inhabit a variety of situations. Several live on moist rocks, damp soil, etc.; many in fresh water, either planktonic, floating, or attached to plants or the bottom, or lying loosely on the bottom; a single species is regularly marine. *A. nidulans* var. *thermalis* Hansg. and *A. bullosa* (Menegh.) Rabenh. occur in thermal springs: Europe (Italy), Asia (Japan), and Africa.

KEY TO THE YELLOWSTONE SPECIES

I. Individual sheaths completely confluent; stratum colorless to yellowish; cells without prominent polar granules　　　　　　　　　*A. saxicola* 1.

II. Individual sheaths distinct; stratum pale blue, pale green, grayish, pinkish, or violet; cells mostly with prominent polar granules.　*A. caldariorum* 2.

1. APHANOTHECE SAXICOLA Naegeli

Gattungen einzelliger Algen, p. 60, 1849.

Stratum slimy gelatinous, formless, colorless or yellowish. Cells cylindrical with rounded ends, 1-2μ in diameter by 2-3 diameters in length, single or in pairs, less often many in a homogeneous slimy matrix. Cell contents homogeneous, blue-green.

Although *A. saxicola* is widely distributed, it is not especially common. It has been reported in North America from Massachusetts (Collins), floating among other algae in Horn Pond, near Woburn; from California (Osterhout), growing on the walls of a reservoir; from Missouri (Drouet); and from British Columbia (Taylor), in alpine pools.

In the Yellowstone, I have found the species in a small pool on the slope of Electric Peak, and in thermal water in the Lower Geyser Basin. In the latter region, it was an incidental to abundant form in the bottom (algal) crust of Firehole Lake. The temperature of the mass of algae was 36° C. while the water itself was slightly warmer, about 36.4° C.; the pH. of the water was 8.3. Firehole Lake, a good-sized, warm, spring-fed pond, has a basal crust of living algae 1-2 cm. thick. The commoner species in this crust were *Lyngbya subspiroides* (of this paper), *Aphano-*

thece saxicola, Synechococcus Minervae var. *maior* (of this paper), and *Phormidium laminosum* (Ag.) Gom. *A. saxicola* has not been found in similar associations elsewhere in the Park, although it may have a wider range of thermal habitats than is indicated.

<div align="center">

2. APHANOTHECE CALDARIORUM P. Richter

Hedwigia, p. 192, 1880.
</div>

Syn.: *Aphanothece muralis* (Tomasch.) Lemm.
      Aphanothece caldariorum var. *muralis* (Tomasch.) Hansg.
      Aphanothece caldariorum var. *cavernarum* Hansg.

Stratum either soft gelatinous to somewhat slimy and extended, or firm gelatinous and verrucose or roughened on the surface, up to 1 cm. or more in thickness, pale bluish, greenish, pinkish, or violet. Cells cylindrical with rounded ends, lightly curved to "S" shaped, often straight; 1.8-3μ in diameter by up to 6 diameters in length, up to 12μ long; usually with distinct, often lamellate individual sheaths. Cell contents pale blue-green to almost colorless, mostly with prominent polar granules. Matrix hyaline, pale violet, flesh-colored, or yellowish. Nannocysts produced by division in three planes, cir. 0.8-1.0μ in diameter by 1-1.5μ long.

The several synonyms listed above represent in part, at least to the authors, distinct forms. The several forms seem to intergrade completely and to be separated mostly by ecological characters. I consider them as complete synonyms. *A. caldariorum* is known from moist, shaded rocks, from near the entrance of caves, and from the windows of greenhouses. Up to now, the species has not been reported either from North America or from thermal situations.

In the Yellowstone its range is very limited. I have found it only in the Boiling River Cave, between Gardiner and Mammoth. Here it was growing on the damp walls and roof of the poorly illuminated passage formed by a now extinct spring. The Boiling River Cave is so named because it is very close to the Boiling River, and has in it, out of sight and inaccessible, the stream of hot water that emerges as the "River." The stream of hot water, deep below the part of the cave that can be reached, gives off hot, humid carbon dioxide containing vapor that fills the cave. The walls and roof are literally always wet deep in the cave, and are uniformly moist near the mouth. The temperature, while not excessive, is high—from 39° C. to 26.8° C.—the former as far back and down as I was able to go; the latter at the mouth. The cave is not only unpleasant to collect in, but in addition to its similarity to a turkish bath, the air is barely, or not at all, able to support ordinary animal life. For

quite an extensive area just within the entrance and mostly on the roof there was a fine growth of *A. caldariorum*. Near the entrance, where the light was moderate (cir. 26.8° C.) and the water supply scant, the growth was a clear amethyst color. A little farther back (cir. 29° C.), where the light was barely strong enough to enable one to read ordinary print and the walls were wet, the growth was pink to flesh-colored. At the extreme limit of growth (cir. 34° C.), where artificial illumination was needed in collecting, the air was foggy and the walls and roof dripping wet; here the algal stratum was pale grey to almost colorless.

The material collected in the Boiling River Cave was almost a pure growth; it gave a wide range in color and texture of the stratum but was unquestionably a single form. It was producing nannocysts in such profusion that in places few vegetative cells could be found. In some places the stratum of the alga was 3 cm. thick, and the surface was so uneven that it formed rudimentary stalactites. (Other Myxophyceae were present but not greatly mixed with the *A. caldariorum*.)

The ability of an alga to grow in such feeble light as the Boiling River Cave admits is an interesting tribute to the satisfactory nature of the other conditions. The uniform moderately high temperature, the regular humidity, the high carbon dioxide content, and the absence of competing species produce an almost ideal situation for the plant.

Several other spring craters and passages in the same vicinity offer an excellent site for careful investigation. It is probable that a gas mask and oxygen tank will have to be included in the equipment of the investigator. In the Boiling River Cave it was necessary to come out for air and to cool off every few minutes. There were in the cave the bones of several animals apparently killed by the unsatisfactory atmosphere.

GLOEOTHECE Naegeli

Gattungen einzelliger Algen, p. 57-59, 1849.

Cells elipsoidal to cylindrical with rounded ends, straight or curved, in small colonies or indefinite often extensive strata. Individual capsules loose, homogeneous or lamellate; matrix concentrically arranged around cell groups, loose, homogeneous or lamellate, colorless to golden or brown, blue, violet, or rarely reddish. Cell division at right angles to the long axis or in more actively dividing colonies often in three planes. Cell contents usually blue-green; pseudovacuoles absent.

The species of *Gloeothece* live either in fresh water or more usually on moist rocks, soil, and other aerial situations. Thermal habits have not previously been noted for the genus.

I. Cells, without sheaths, less than 3.6μ in diameter.
   1. Cells cylindrical, up to 6 diameters in length.   *G. linearis* 1.
   2. Cells ovoid or very short cylindrical, less than 2½ diameters in length.
                                          G. Goeppertiana 2.
II. Cells, without sheaths, greater than 3.6μ in diameter.
   1. Tegument colorless to golden brown, lamellate or not; cells, without
     sheaths, 4–5μ in diameter.   *G. rupestris* 3.
   2. Tegument always colorless, very distinctly lamellate; cells, without
     sheaths, 5–6μ in diameter.   *G. rupestris* var. *tepidariorum* 3A.

1. GLOEOTHECE LINEARIS Naegeli

Gattungen einzelliger Algen, p. 58, 1849.

Stratum gelatinous, olive-green to dull yellow. Cells mostly single, 1.5–2.5μ in diameter by 9–18μ in length, cylindrical, straight, curved or twisted, pale blue-green. Individual sheaths colorless, broad, homogeneous, and frequently confluent into an amorphous or almost amorphous colonial matrix, often almost invisible.

Growing on moist rocks, in greenhouses on the damp soil or frames, and less often in pools or rarely planktonic, *G. linearis* is widely distributed and quite common. There are few published records of its occurrence in North America.

In the Yellowstone it occurs quite generally on moist, shaded cliffs. In the White Elephant Grottoes at Mammoth it was found on the moist rock walls at a temperature of 14° C., slightly warmer than would be expected in the absence of some thermal spring influence. It was mixed with other Myxophyceae typical of such a shaded situation. A few of the species with it are regularly found at higher temperatures. The plant, as far as is known, is clearly a non-thermal species, not tolerating even warm situations.

2. GLOEOTHECE GOEPPERTIANA (Hilse) Forti

in De Toni, Sylloge Algarum 5, p. 62, 1907.

Stratum extended, soft gelatinous, blue-green to dull brown. Cells ellipsoidal, 2.7–3.2μ in diameter by cir. 2 diameters in length, 4–8μ long, blue-green, mostly 2–4 in a group, less often with many in a single family. Tegument colorless, made of concentrically placed layers; individual sheaths lamellate or obscurely so.

There are few records for *G. Goeppertiana*. Up to the present it has been reported only from moist earth in Europe. In the Yellowstone it occurs as an incidental form around the edge of pools and rills in the

Lower Geyser Basin. Its known range includes Ojo Caliente Spring, Five Sisters Springs runoff, and several unnamed springs in the Lower Geyser Basin, and Spray Geyser rill in the Twin Buttes Region. It has been found up to 31° C. and at a pH. of from 8.2 to 9.05.

3. GLOEOTHECE RUPESTRIS (Lyngbye) Bornet

in Wittrock et Nordstedt, Algae exsiccatae No. 339, 1880.

Plant mass extended and olive to blue-green, more frequently poorly developed, and mixed with other algae. Colonies mostly of 2, 4, or 8 cells. Cells ellipsoidal to cylindrical, 4–5.5μ in diameter, and up to 3 diameters in length, 6–15μ long, blue-green. Sheaths colorless or on surface of the stratum golden to brown, lamellate or almost homogeneous, often somewhat confluent in the interior.

The usual habitat is on moist to wet rocks and cliffs or soil. It frequently occurs in greenhouses. In the United States it has been reported from San Leandro, California (Osterhout and Gardner), where it was found on dripping boards.

In the Yellowstone, I have found it only in the Bijah Group of Springs, growing on the damp vertical sides of fumaroles and pots. In this region it was quite abundant within certain temperature limits. The alga occurred at from 34.5° C. down to 21° C. (the coolest of the pool edges). It was abundant from 24° C. to 32° C. The pH. of the damp earth and rock it lived on was 6.2–6.6.

3A. GLOEOTHECE RUPESTRIS (Lyngbye) Bornet

var. TEPIDARIORUM (A. Braun) Hansgirg

Prodr. Alg. Fl. Bohmen 2, p. 134, 1892.

Cells 5–6μ in diameter by 8–16μ in length. Sheaths very distinctly lamellate, colorless. Otherwise as in the species.

The variety grows mostly in situations similar to those occupied by the species, but only occasionally with it. In the United States it is known from Rhode Island, where it was found on the woodwork of a dam (Osterhout).

In the thermal springs of the Yellowstone this variety is much more common and widely distributed than the species proper, although at best it is an incidental form. It occurs on moist, warm cliffs, rocks, and soil, and on damp sinter and travertine quite generally in the cooler ranges. Its presence has been noted in the Mammoth Hot Springs: White Elephant Grottoes (abundant in places at cir. 28° C.), Jupiter Terrace run-

off; Boiling River Cave; Twin Buttes Region: edge of stream (31.3° C.); Lower Geyser Basin: moist rocks near Hot Lake, cliff below spring on Nez Perces Creek; Upper Geyser Basin: seeps on Firehole River; and elsewhere.

<div align="center">GLOEOCAPSA Kützing</div>

<div align="center">Phyc. gen., p. 174, 1843.</div>

Cells spherical, in small colonies, less often in colonies of many; colonies single or united into a stratum. Individual capsules loose, homogeneous or lamellate; matrix concentrically arranged around cell groups, loose, homogeneous or lamellate, colorless to golden, orange, brown, violet, or reddish. Cell division in three planes. Cell contents usually blue-green; pseudovacuoles absent. Nannocysts present in some species. Resting cells often present.

The species of this large and important genus occur in a wide variety of habitats: the majority living on moist or almost dry rocks, soil, etc.; fewer in fresh water, either on the bottom of quiet pools and streams, or planktonic; one or two in brackish water or marine, especially on rocks and woodwork in the intertidal zone; some on moist soil and frames in greenhouses; and several in warm springs. The "thermal" species, without exception, are found only at comparatively low temperatures and are probably mostly transitional forms. Five species, up to now, have been credited to such warm habitats. *G. thermalis* Lemm. is known from a spring on Mauna Kea, Hawaii (Lemmermann), and a hot sulphur spring near Budapest, Hungary (Strøm). *G. arenaria* (Hassal) Rabenh. is known from hot and sulphur springs in Europe, and from non-thermal sources in many regions, including several in North America. *G. gelatinosa* Kütz. has a rather similar group of sources credited to it, although it is less well known in North America. *G. montana* Kütz. occurs widely on moist rocks, walls, among mosses, and sometimes in pools or slow streams; the only record of the species from thermal sources is that of Tilden for Yellowstone Park. The species is not otherwise credited to North America. *G. violacea* (Corda) Rabenh. has been reported from a Yellowstone thermal spring by Tilden. Probably her record is to be referred to *G. compacta* Kütz.

In this study ten species of *Gloeocapsa* were found in the Yellowstone springs. With the exception of *G. compacta*, all were incidental forms. They occurred quite widely at temperatures of 35° C. and below, and quite infrequently above 35° C. They were growing, with few exceptions, as terrestrial forms, on the moist edges of springs, on seepy cliffs and rock ledges, especially on travertine deposits.

I. Sheaths colorless even in old exposed colonies.
   1. Sheaths mostly lamellate.
      A. Lamellation of the sheaths indistinct, more or less confluent.
         a. Cells, without sheaths, greater than 3μ in diameter.

                                        G. arenaria 1.
         b. Cells, without sheaths, less than 3μ in diameter.

                                        G. gelatinosa 2.
      B. Lamellation of the sheaths distinct.
         a. Cells, without sheaths, less than 5μ in diameter.
           *. Sheaths thick. "wide".   *G. fenestralis* 3.
           **. Sheaths thin, "narrow".   *G. montana* 4.
         b. Cells, without sheaths, greater than 5μ in diameter.

                                      G. decorticans 5.
   2. Sheaths mostly homogeneous, not lamellate.   *G. calcarea* 6.
II. Sheaths pigmented at least in part in older colonies, often colorless when young.
   1. Sheaths yellowish to brownish, golden or orange, often colorless in part.
      A. Cells, without sheaths, 1.5–3.0μ in diameter.   *G. dermochroa* 7.
      B. Cells, without sheaths, 6–11μ in diameter.   *G. rupestris* 8.
   2. Sheaths reddish or violet, often colorless in part.
      A. Sheaths orange-red, golden-red, red, or reddish-brown.

                                      G. stegophila 9.
      B. Sheaths violet.   *G. compacta* 10.

1. GLOEOCAPSA ABLNARIA (Hassal) Rabenh.

Flora Europaea Algarum 2, p. 39, 1865.

Stratum soft gelatinous, olivaceous, often poorly developed. Cells, without sheaths, 3–4.5μ in diameter; with sheaths, 6–17μ; colonies up to 43μ in diameter. Capsules spherical or ovoid, thick, colorless, indistinctly lamellate. Cell contents finely granular or often homogeneous, blue-green to greenish or brownish.

The majority of the European records for *G. arenaria* credit it to warm springs and mineral springs; the records of its occurrence in North America are chiefly on flower pots in greenhouses, and on moist rocks. It is known from Maine (West), Minnesota (Lilley), Iowa (Buchanan), and Nebraska (Saunders). It has not previously been recorded from the Yellowstone, or from North American hot springs. It occurs quite frequently in the Mammoth Hot Springs region on wet travertine detritus at temperatures up to $27°$ C., mostly in alkaline situations between pH. 7.6 and 8.1. Its presence has been noted in the Stygian Caves, White Elephant Grottoes, Boiling River Caves, Jupiter Terrace, White Elephant Back, and Angel Terrace. It was most abundant at quite low temperatures (cir. $14°$ C.) and was of little prominence above $20°$ C.

2. GLOEOCAPSA GELATINOSA Kützing

Phyc. gen., p. 174, 1843.

Stratum firm gelatinous, often mammillate or raised. olive to green, submerged or on moist rocks. Cells, without sheaths, 2–2.8μ in diameter, with sheaths 6.2–10μ in diameter. Colonies about 25μ in diameter, or often smaller. Sheaths colorless, moderately narrow, lamellate when old, but indistinctly so. Cell contents homogeneous, blue-green.

Occurring widely in warm springs, *G. gelatinosa* is little known in North America. Wolle's record of 1877 gives no field data and omits the locality, and it is on his single record that the presence of the species in United States is based. In the Yellowstone I have found the species in good quantity in the Stygian Caves, Mammoth Hot Springs. In this shallow grotto the shaded moist travertine rock is little warmer than it would be in a non-thermal locality. A slight seepage of warm water trickles over part of the walls and keeps them uniformly moist to wet. The species occurred there at temperatures of from 12.8° C. to 24° C. and at a pH. of 8.1. It was growing mixed with *Gloeothece rupestris* Kütz., *Gloeothece linearis* Naeg., *Gloeocapsa arenaria* (Hass.) Rab., *Chroococcus minutus* (Kütz.) Naeg., *Schizothrix cyanea* Naeg., *Phormidium fragile* (Menegh.) Gom., and *Oscillatoria geminata* var. *tenella* (of this paper).

3. GLOEOCAPSA FENESTRALIS Kützing

Phyc. gen., p. 173, 1843.

Stratum thin, extended, soft gelatinous, mostly irregular and uneven. greenish. Cells, without sheaths, 2.2–3.4μ in diameter; with sheaths 7–15μ. Sheaths thick to very thick, colorless, distinctly lamellate, often peeling. Cells grouped into colonies 16–48μ in diameter. Cell contents homogeneous or granular. pale blue-green.

This species is not especially well known. It has been found in Europe on window panes in greenhouses; and in Fukien Province, China (Gardner). In the United States the only record I am acquainted with is from Put-in Bay, Lake Erie, Ohio (Snow). In the Yellowstone, the species has been found only in the White Elephant Grottoes, Mammoth Hot Springs at 26° C. and pH. 8.1. In that site it formed an almost pure growth on the damp shaded wall of the shallow cave. Until more data is available the species may be considered as probably a non-thermal one, favoring slightly warm, shaded situations.

4. GLOEOCAPSA MONTANA Kützing

Phyc. gen., p. 173, 1843.

Plant mass amorphous, soft gelatinous to flocculent, often thickish, pale yellowish-green to clear blue-green. Cells, without sheaths, 2–5μ in diameter, single or in groups of 2 to 4, rarely larger, pale blue-green. Tegument hyaline, distinctly lamellate or less often confluent and mostly homogeneous. Colonies up to 39μ in diameter.

Growing on moist rocks, damp soil and sometimes in pools or very sluggish streams—the species is probably widely distributed. Tilden (1896) has reported it from warm overflow water in the Lower Geyser Basin, Yellowstone Park. In the present investigation the plant has been found regularly on moist, warm ledges and travertine cliffs in the Mammoth Hot Springs. Its distribution there includes the White Elephant Grottoes (19–26° C.), Stygian Caves (13.1° C.), and the lower part of the stream carrying water from Jupiter Terrace (moist travertine edges, and log partly in stream) (18–31° C.). The pH. of the situations it was found in averaged around 8.2. The species has not been noted elsewhere, although from Tilden's record it may occur in the Geyser Basins, which furnish situations of similar degrees of acidity and temperature. On the whole the species is best considered as a non-thermal form, invading the lower thermal ranges.

5. GLOEOCAPSA DECORTICANS (A. Br.) P. Richter

Syn.: *Chroococcus decorticans* A. Braun, Betr. u. d. Erschein. Verjüng in der Natur, p. 194, 1851.

Cells spherical or subovoid, single or in pairs, or less often in fours; without sheaths cir. 6μ in diameter by 6–8μ long, blue-green. Single-celled colony cir. 19 by 21μ; two celled colony cir. 22 by 30μ. Sheaths thick, colorless, distinctly lamellate, often peeling.

I am following Wille in considering this species as a *Gloeocapsa* rather than as a *Chroococcus*.

The commoner habitats for it are on submerged wood and in standing waters; its known distributions includes Europe and North America (Wolle, on submerged timbers in Pennsylvania). The only site discovered for it in the Yellowstone was Soda Spring, Mammoth Hot Springs region, where it occurred rather rarely at 30° C. and pH. 6.5, in the shallow stagnant spring pool. Because of its presence in this single, quite unique spring, there is no reason for assuming that it has a wider range in the thermal springs of the Park. The species is primarily non-thermal.

6. GLOEOCAPSA CALCAREA Tilden

List of Freshwater Algae collected in Minn. 1896 and 1897, Minn. Bot. St. 2, p. 29, 1898.

Stratum often incrusted with lime (or silica), if unincrusted gelatinous and roughened above, extended, grayish to blue-green. Cells, without sheaths, 2–3.5μ in diameter; with sheaths, 6–9μ in diameter; cell contents mostly granular, blue-green. Sheaths colorless, mostly homogeneous or rarely feebly lamellate, often rather thin. Cells united into colonies of mostly 4–16; colonies 25–50μ in diameter.

I have found the incrustation to be much less constant and reliable than Tilden's description implies. In her description the cell diameter was omitted. I have added it to the diagnosis above.

The single record of the species from Osceola, Minnesota (Tilden), appears to be the summary of data on the distribution of the species. At that place the plant was reported to have been found on boards receiving a continual dripping from a spring trough. In the Yellowstone it occurs commonly in the Lower Geyser Basin on wet sinter, mostly incrusted with silica; less often in the Upper Geyser Basin, where it was found usually with less incrustation. In the Lower Basin it was found on the cone of White Dome Geyser (19.2° C., pH. 8.4), and by several seeps and moist sinter outcrops; in the Upper Basin on the sinter banks of the Firehole River (12.8–26° C., pH. 8.3–8.6). It is apparently largely non-thermal, being most abundant around 20° C.

7. GLOEOCAPSA DERMOCHROA Naegeli

Gattungen einzelliger Algen, p. 51, 1849.

Syn.: *Gloeocapsa punctata* Naegeli, Gatt. einzell. Alg., p. 51, 1849.
　　　Gloeocapsa biformis Ercegovic, Acta Bot. inst. Bot. R. univ. Zagreb. 1, p. 80, 1925.

Cells, without sheaths, 1.5–3μ in diameter; with sheaths up to 8μ; blue-green, united into colonies up to 50μ in diameter or masses often of considerable size and containing many cells. Sheaths not lamellate, golden to brownish at maturity, often colorless when young. Resting cells with firm thin dark capsules.

I agree with Ercegovic (1925) that *G. dermochroa* Naeg. and *G. punctata* Naeg. are the same species. As he pointed out, *G. punctata* is the "young," unpigmented stage, while *G. dermochroa* is the "older" pigmented form of the same plant. The two forms were described as species by Naegeli in the same paper (l.c.) and even on the same page. I do not agree at all with the treatment Ercegovic has given the matter

in renaming the species *G. biformis* Erc. 1925. Inasmuch as Naegeli gave a reasonably accurate diagnosis of the mature stage under the name *G. dermochroa,* the immature form should certainly be placed in that species. Technically, of course, the description for *G. dermochroa* was neither accurate nor diagnostic but, if the same handling was accorded all similar situations, the large number of changes in nomenclature would be confusing and unnecessary. It has been generally accepted that additions to our knowledge of the life histories and structure of species do not introduce the need for taxonomic shifts unless such are of value in clarifying or correcting possible former errors.

G. dermochroa is widely distributed, growing on rock cliffs. In North America it is not well known. Snow (1903) reported it (as *G. punctata*) from Put-in-Bay, Lake Erie, Ohio. In the Yellowstone the species has been found quite widely at low temperatures. In the Mammoth region it occurs on moist travertine up to about 34° C. and about pH. 8.2; in the Twin Buttes Region it has been found on the banks of the Spray Geyser overflow (on damp sinter) at up to 39° C. and at a pH. of from 8.8–9.0; in the Upper Geyser Basin in several sites on moist rock at temperatures up to 43° C. The species shows considerable resistance to warm conditions and locally is approaching thermal habitats closely.

8. GLOEOCAPSA RUPESTRIS Kützing

Tab. phyc. 1, pl. 22, 1845-9.

Stratum grayish-black to black, crustaceous, often hard. Cells, without sheaths, 6–11μ in diameter, grouped into colonies 15–75μ in diameter; cell contents dull to brownish blue-green. Sheaths thick, golden brown to brown, often very pale or even colorless on the outer part of colony or cell groups, very distinctly lamellate. Resting cells with thin, smooth dark brown walls; cir. 15μ in diameter.

Occurring on moist rocks, the species has a worldwide distribution. In North America it has been found in several localities and is well known. There have been no previous records for it from the Yellowstone. Its range in the Yellowstone does not carry it into thermal situations, although it approaches them quite closely. It has been found on wet ledges and wet cliffs in the Gallatin Mountains on calcareous rock (completely non-thermal); and on travertine ledges and walls in the Mammoth Hot Spring region. The records for it there include the Stygian Caves (10.8° C. to 21° C.); White Elephant Grottoes (19.4° C.); bank of Gardiner River at point of spring seepage near Boiling River (22.6° C.); and damp sides of the Narrow Gauge Terrace (16.4°

C.). It was found at a pH. of 7.65–8.2. The species is non-thermal and was most abundant in shaded sites.

9. GLOEOCAPSA STEGOPHILA (Itzigs.) Rabenh.

Krypt. Fl. v. Sachsen, p. 72.

Cells, without sheaths, 3–4μ in diameter; with sheaths, 4.5–8μ, united into colonies of 2 to 16 cells, blue-green. Sheaths golden, orange-red, or reddish, mostly not lamellate. Resting cells with dark reddish brown, firm, thin sheaths; cir. 5μ in diameter.

The usual habitat for the species seems to be on moist wood, soil, and rock. There are no records for it, to my knowledge, from either North America or from thermal situations. In the studies carried on in the Yellowstone it has been found a single time, and then in very small quantity. This collection was from rocks kept warm and moist by steam from a hot spring in the Meadow Spring group. It was growing in the stratum of *Colteria funebris* (of this paper) at 38° C. With this single observation no conclusions can be drawn as to its place in the Yellowstone flora, other than that it is rare.

10. GLOEOCAPSA COMPACTA Kützing.

Tab. phyc., pl. 36, Fig. 4, 1845-49.

Syn.: *Gloeocapsa violacea* (Corda) Rabenhorst var. *compacta* (Kützing) P. Richter.

Stratum purplish-black to violet-brown, extended, gelatinous, smooth, or beaded and up to 3mm. thick. Cells, without sheaths, 2.1–2.6μ in diameter; few to many in a broad, soft capsule; cell contents homogeneous, blue-green. Sheaths homogeneous or sometimes faintly lamellate, pale violet, reddish violet, or often almost colorless (when not in masses). Resting cells with deep violet-brown or violet, firm, tough capsules and almost opaque cells, cir. 3μ in diameter.

The relationship between *Gloeocapsa compacta* Kütz. and *G. violacea* (Corda) Rabenhorst has been the subject of some difference in opinion. Forti, in DeToni, places *compacta* as a variety of *G. violacea*. Geitler, in Rabenhorst, recognizes *G. compacta* as a valid species and questions the existence of *G. violacea* as an entity. Tilden has recorded *G. violacea* from the Yellowstone (Valley of the Nez Perces Creek, Lower Geyser Basin, mixed with *Synechococcus aeruginosus* Naegeli and *Hypheothrix calcicola* (Ag.) Rab., the three forming "Algal Stalactites" in a warm "cave" formed by a geyser cone). Her description is not sufficiently detailed to enable one to be certain of the form she found but it remains

as an open possibility that she may have had *G. compacta.* Setchell has reported *G. violacea* from Alaska, and Collins, from Gaylordsville, Connecticut. The status of their records does not have any bearing on the occurrence of *G. compacta* in the present report.

G. compacta Kütz. is a well-known European species, occurring on moist cliffs, bark of trees, and less often in greenhouses. Its presence in North America has not been previously noted. In Yellowstone Park it appears to be rather widespread, but only rarely is found in abundance. Its presence has been noted in the Upper Geyser Basin in the following places: Orange Pool, 24° C., pH. 8.6; Wave Spring, 27° C., pH. 8.6; Chromatic Pool, 31° C., pH. 8.95 (no. 384); seep on bank of Firehole River opposite Grand Geyser Group, 29.3° C., pH. 8.75; in the Biscuit Basin: Bubble Pool, 28° C., pH. cir. 8.8. (no. 373); Midway Basin: Excelsior Geyser Crater, damp wall, 27° C.; Lower Geyser Basin: Firehole Lake Bank, 26° C.; West Thumb: unnamed spring, 28.4° C. Its greatest abundance was noted at Bubble Pool, Biscuit Basin, and its habitat there may be taken as typical of its occurrence in Yellowstone. The growth of the plant was sharply confined to the wet sinter rock, and it was found only outside of the pool rim where the temperature was moderate. No encrustation was encountered with it, although where it was mixed with *Calothrix Kuntzei* P. Richter, it gave that appearance. The temperature range observed was from 24–31° C., the pH. range from 8.6–8.9. It can be seen that *G. compacta* is essentially a non-thermal alga, gaining a foothold in the cooler situations only.

CHROOCOCCUS Naegeli

Gattungen einzelliger Algen, p. 45, 1849.

Cells spherical or following division hemispherical, quadrant- or octant-shaped or at least flattened on adjacent faces for a time following division, occasionally single or usually either in colonies of mostly 2–4, less often up to 8 or 16, or in larger colonies of several to many cells; colonies not often forming a definite stratum. Sheaths close fitting, concentrically placed, lamellate or not, either thick ("broad" or "wide") or thin ("narrow"), colorless or variously colored; sheaths firm or sometimes mostly confluent. Cell division in two or usually three planes. Cell contents usually blue-green but sometimes violet, olive-green, orange, or yellowish; pseudovacuoles in few species. Resting cells and planococci unknown.

The species of *Chroococcus* inhabit situations similar to those of the species of *Gloeocapsa.* The largest number are found on moist rocks, etc.; several occur in standing waters, especially mixed with other algae, or almost as often, planktonic; a few are found regularly in greenhouses;

a very limited number in brackish (rarely in salt) waters; and at least four species have been found to occur at times in warm and hot springs. *C. turgidus* var. *thermalis* (Kütz.) Rabenh. and *C. membraninus* (Menegh.) Naeg. have been reported from European thermal springs, and *C. minor* (Kütz.) Naeg. from a hot sulphur spring (sulphur or sulphide containing?). *C. varius* A. Braun was recorded from a warm spring at Lo Lo, Montana, by Griffiths; and *C. thermophilus* described from a hot spring in California by Wood. (Wood's description was incomplete and cannot be accurately placed.) These are the only known North American occurrences of thermal species of *Chroococcus*.

Of the Yellowstone species several occur in quite warm waters; none have been found above 50° C. The species are in part quite abundant in their occurrence and widespread in the many springs. The most outstanding feature of the group is the well-marked tendency for certain species to occur on and in the strata of gelatinous Myxophyceae, especially *Phormidium* and *Mastigocladus*.

<center>KEY TO THE YELLOWSTONE SPECIES</center>

I. Sheaths lamellate.
  1. Sheaths distinctly lamellate.
    A. Cells, without sheaths, greater than 5μ in diameter; sheaths thick, never peeling.   *C. yellowstonensis* 1.
    B. Cells, without sheaths, under 5μ in diameter; sheaths very thick, splitting and peeling.   *C. tenacoides* 2.
  2. Sheaths obscurely lamellate.   *C. turgidus* 3.
II. Sheaths not lamellate.
  1. Cells single or after division in small colonies, of at most eight.
    A. Cells, without sheaths, 4μ in diameter or greater.
      a. Cells of 2–4-celled colonies closely packed and broadly flattened on adjacent faces.   *C. turgidus* var. *thermalis* 3A.
      b. Cells not closely appressed; slightly flattened.
        *. Sheaths colorless.
          !. Sheaths thick or moderately thick; cells, without sheaths, $5–10\mu$ in diameter.   *C. minutus* 4.
          !!. Sheaths thin; cells, without sheaths, $4.4–5.2\mu$ in diameter.   *C. minutus* var. *thermalis* 4A.
        **. Sheaths yellowish brown.   *C. minutus var. fuscus* 4B.
    B. Cells, without sheaths, $3–4\mu$ in diameter.   *C. minor* 5.
  2. Cells in larger colonies or indefinite masses.
    A. Cells, without sheaths, 2μ or greater in diameter; free-living.
        C. minimus 6.
    B. Cells, without sheaths, 2μ or less in diameter; endophytic.
        C. endophyticus 7.

1. Chroococcus yellowstonensis, sp. nov.

Cells single or in colonies of 2–8 cells, mostly in twos, among and in the strata of other algae, dull blue-green, with granular contents, or often homogeneous or with a single large granule; without sheaths 5–8μ in diameter, with sheaths 8–14μ in diameter. Tegument colorless, distinctly lamellate, up to 4μ thick. Two-celled colonies 10–14μ by 13–17μ; cells of two-celled colony broadly flattened on adjacent faces, 5–7μ in length.

Chroococcus yellowstonensis is similar to *C. turgidus* (Kütz.) Naeg. It differs from it by its smaller and more definite size; thicker and more distinctly lamellate tegument, and by its occurrence on and in the strata of gelatinous algae.

It has been found at West Thumb (no. 448) in the thallus of *Phor-*
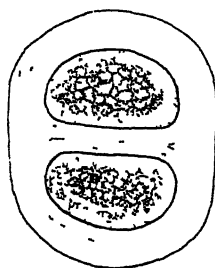
FIG. 5 —*Chroococcus yellowstonensis* (×2000).
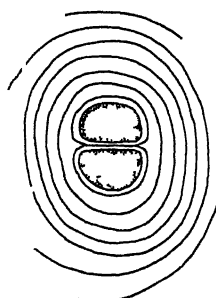
FIG. 6 —*Chroococcus tenacoides* (×2000)

midium laminosum (Ag.) Gom. at 37° C.; at Mammoth Hot Springs (no. 93—type, and no. 95) on the damp roof and walls of the White Elephant Grottoes at 19–26° C.; and in the Upper Geyser Basin (nos. 436, 437, 438) on Bijou Geyser Cone at temperatures ranging from 37–42° C., mostly on species of *Phormidium*. It seems to be limited to damp and wet habitats, and has not been found submerged. At the White Elephant Grottoes it was, in the first collection, on and in a stratum of *Schizothrix calcicola* (Ag.) Gom., along with *Gloeocapsa montana* Kütz. and *G. fenestralis* Kutz.; in the other, on and in *Symploca cavernarum* (of this paper), along with *G. fenestralis* Kütz.

2. Chroococcus tenacoides, sp. nov.

Cells mostly in twos, often in fours, and occasionally single; on and in the strata of other Myxophyceae; pale blue-green to olive-green, with homogeneous or finely granular contents, without sheaths 4.0–5.0μ in diameter, with sheaths 10–18u in diameter. Tegument colorless, thick (up to 6μ), very distinctly lamellate, the outer lamellae rupturing and peeling. Two-celled colony 10–18μ

in diameter by 12–22μ in length; cells of two-celled colony strongly flattened on adjacent faces, 3–4μ in length.

Chroococcus tenacoides falls in the *C. turgidus* plexus of species, but is one of the most extreme of the group. The species showing the greatest resemblance to it are *C. yellowstonensis* (of this paper) and *C. tenax* (Kirch.) Hieron. From *C. yellowstonensis* it may be differentiated by its thicker, rupturing and peeling, and much more sharply lamellate sheaths, as well as by its slightly smaller cell size and (in the 2–4 celled colonies) shorter cells. From *C. tenax* it is separated by its much smaller size and constantly colorless tegument.

The species has been found only in the Spray Geyser and Imperial Geyser Overflow, in the Twin Buttes Region. Its distribution is not well known in even these sites, and the species seems to be constantly rare or at most occasional. The type (no. 429) is from the junction of Spray Rill and Imperial Creek, growing in shallow water at 31° C. and pH. 9.05; it was growing among a mixture of *Oscillatoria geminata* Menegh. and *Phormidium laminosum* (Ag.) Gom., and was at best occasional.

3. CHROOCOCCUS TURGIDUS (Kütz.) Naegeli

Gattungen einzelliger Algen, p. 46, 1849.

Cells single or mostly in colonies of 2–4, rarely 8, clear blue-green, olive-green or golden, without sheaths 8–32μ in diameter, with sheaths 13–40μ. Cells broadly flattened on adjacent faces and close. Sheaths colorless, indistinctly lamellate. Cell contents homogeneous or granular.

The species is cosmopolitan. In North America it has been generally confused with the similar *C. turgidus* var. *submarinus* Hansgirg to such an extent that it is difficult to interpret the many records. It occurs chiefly on wet rocks, in boggy pools, and among other algae.

In the Yellowstone it is to be found in its usual habitats quite regularly, and infrequently it invades subthermal situations. Its most notable occurrence was at Mammoth Hot Springs on the damp walls of the Stygian Caves (no. 150), where it reached the temperature of 22° C. (pH. 7.7), and was not infrequent.

3A. CHROOCOCCUS TURGIDUS (Kützing) Naegeli

var. THERMALIS (Kützing) Rabenhorst

Fl. Eur. Alg. 2, p. 33, 1865.

Sheaths homogeneous or at maturity very feebly lamellate (not evident without staining). Cells 6–10μ in diameter. Otherwise as in the species

Geitler (1930) was unable to note the small size of the cells upon an examination of the type specimen (Rabenhorst: Alg. Eur. No. 1413). It is quite possible that since *C. turgidus* and this variety of it overlap in cell size, this difference may be of little consequence. The two forms are very close, but clearly distinct. The var. *thermalis* was described from an European hot spring. Its presence in North America has not been previously noted.

In the Yellowstone it occurs generally on the moist and wet shaded, warm travertine cliffs and ledges, and shallow shaded tepid pools in the Mammoth Hot Springs formation. It has not been found as an abundant form, but it is very characteristic at temperatures of 15–30° C. The limits of temperature range observed were 13.1° C. and 36.6° C.; and the range of acidity pH. 6.5–8.3. Its known occurrence includes: White Elephant Grottoes (no. 101), Stygian Caves (no. 148), Jupiter Terrace Slope, Narrow Gauge Terrace, Soda Spring (no. 128), and other sites.

4. CHROOCOCCUS MINUTUS (Kützing) Naegeli

Gattungen einzelliger Algen, p. 46, 1849.

Cells single or in colonies of 2 to 4, pale blue-green, spherical, without sheaths 5–10μ in diameter, with sheaths 7–15μ in diameter. Sheaths colorless, homogeneous, and neither lamellate nor concentrically arranged. Colonies mostly ovoid, 6–9μ in diameter by 10–15μ long. Cells feebly flattened on adjacent faces, distant. Cell contents either homogeneous or granular.

Although widely distributed and common in standing water, often planktonic, and at times in brackish water, *C. minutus* has not been frequently reported in North America, and it has not before been reported from warm waters.

In the Yellowstone the plant is widely distributed. It has been found in Upper Geyser Basin: warm cliff by Firehole River on wet rocks; Lower Geyser Basin: White Dome Geyser (no. 405) at 19.2° C. and pH. 8.4, and Firehole Lake at 36° C. and pH. 8.3, on the bottom crust; Firehole River at Upper Geyser Basin (no. 337) at 17.8° C. and pH. 7.2; Mammoth Hot Springs: Orange Spring Mound, Jr. (no. 84) at 30.2° C. and pH. 8.0, Jupiter Terrace (no. 238) at 20° C. and pH. 8.3, Stygian Caves (no. 145) at 14° C. and pH. 8.1; and in the Chocolate Pots in the Gibbon Canyon (no. 280) at 29.4° and pH. 6.6; and elsewhere. The Yellowstone material varies a little in the width of the sheath and possibly might be considered to be intermediate between typical *C. minutus* and *C. minutus* var. *obliteratus* (Richter) Hansg. It seems possible that the width of the sheath varies with the type and

amount of water available. When growing submerged or planktonic, the sheath is frequently broader and more typical, but in merely moist situations the sheath is narrow and of the *obliteratus* type. Thus the var. *obliteratus* is to be considered as form *obliteratus* (and of no taxonomic value). In pure culture it has been possible (with the Yellowstone material) to affect the width of the sheath by varying the consistency and type of culture medium employed. *C. minutus* is a species that is typically non-thermal but able to withstand temperatures slightly in excess of 30° C. It is widespread but rarely abundant in the Yellowstone springs.

4A. CHROOCOCCUS MINUTUS (Kützing) Naegeli

var. thermalis, var. nov.

Cells single or in pairs, never in fours; without sheaths 4.4–5.2µ in diameter. Sheaths narrow, 0.5–1.0µ in thickness. Cell contents with a few (mostly 2–3, rarely none) large prominent granules, and mostly finely granular or less often homogeneous protoplasm. Otherwise as in the species.
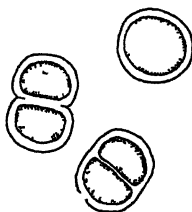
FIG 7 — *Chroococcus minutus* var thermalis (×1330)

FIG 8 —*Chroococcus minutus* var fuscus (×1000).

The variety *thermalis* comes close to form *obliteratus* of the same species in sheath characters. The regular, small cell diameter, and much narrower sheaths separate it from this narrow sheathed form of the species quite sharply.

Up to the present only two collections of the variety have been made. It was found growing in a small pool at the edge of Soda Spring, in the Mammoth Hot Springs region (type: no. 126) at 42° C. and pH. 6.1. In this pool it was present in considerable abundance, as a secondary form growing with other algae. The pool had a very high mineral content and was choked with a growth of various Myxophyceae: *Oscillatoria Cortiana* (Menegh.) Gom., *Spirulina labyrinthiformis* Menegh., and *Phormidium tenue* (Menegh.) Gom.; among these the *C. minutus*

thermalis occurred.   The second collection (no. 320) is from a seep in Imperial Geyser Crater, Twin Buttes Region, growing at 41° C. on moist mud, with various filamentous Myxophyceae. This variety, in pure culture, was able to withstand and grow at temperatures up to 54° C., while the species stopped growth below 40° C.   The two forms thus have physiological as well as morphological differences.

4B. CHROOCOCCUS MINUTUS (Kützing) Naegeli

var. fuscus, var. nov.

Sheaths tan to golden brown.   Otherwise as in the species.

The known distribution of this variety is not extensive.   It has been found in the Mammoth Hot Springs in a majority of the many springs. The type (no. 84) is from Orange Spring Mound, Jr., at 30° C. and pH. 8.0.   It has also been found in Orange Spring Mound, Hymen Terrace, Angel Terrace, Jupiter Terrace, Minerva Terrace, Diana Terrace, White Elephant Back, Main Terrace, and a few less important springs, always at or near the termini of small rills or on damp edges of the cooler streams.   Its temperature range, as observed, is from 23° C. to 46° C., its pH. range from 7.2–8.4.   The species is chiefly an incidental form, mostly in the *Calothrix* and *Calothrix-Diatom* formations.   While less widespread in the Yellowstone, the var. *fuscus* is more typically thermal than the *C. minutus*.   Their ranges overlap slightly; the variety becomes less important at lower temperatures, the species more important.

5. CHROOCOCCUS MINOR (Kützing) Naegeli

Gattungen einzelliger Algen, p. 47, 1849.

Stratum soft, slimy gelatinous, dull blue-green to olive-green. Cells, without sheaths, 3–4µ in diameter, single and in twos, less often in fours.   Tegument slimy, scarcely visible, colorless: cell walls thin, hyaline.   Cell contents homogeneous, usually pale blue-green.

Although known from many localities in Europe, *Chroococcus minor* has been reported only a few times from the Western Hemisphere.   The North American records include Nebraska (Bessey) and St. Vincent and Dominica in the West Indies (Elliott).   It has been found in standing water, on moist rocks, tree trunks, etc., and in hot sulphur springs.   Its presence in Yellowstone Hot Springs is not surprising.

I have found the species in the Upper Geyser Basin in a stratum of *Phormidium laminosum* (Ag.) Gom. in a pool on Bijou Geyser Cone (no. 439) ; and in stalactites, chiefly of the same alga, in a nearby site,

growing at temperatures of 36.8° C. and 32.5° C. and at a pH. of 8.95
in each case; in the Twin Buttes Region: Spray Geyser runoff (nos. 418
and 427) at 37.4° and 39.3° C. and at pH. 8.95 and 9.0, among *Phormidium laminosum;* and in the Bijah Group (nos. 118 and 121) at 25° C.
and at 34.5° C., pH. 6.2, among various Myxophyceae. The alga was
frequent in three sites, occasional in the others.

6. CHROOCOCCUS MINIMUS (Keissler) Lemmermann

Arch. f. Bot. 2, p. 102, 1904.

Cells united into spherical or ellipsoidal colonies of many cells; without
sheaths 2–3μ in diameter, with individual sheaths 4–5μ in diameter. Sheaths
colorless, homogeneous. Cell contents homogeneous, blue-green.
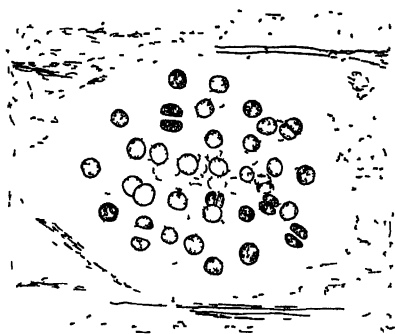
FIG. 9.—*Chroococcus endophyticus,* in
stratum of *Phormidium* (×1470)

C. minimus is very imperfectly known. It has not been previously
recorded from thermal situations; up to now it has not been known from
North America.

Only a single collection of the plant has been made in the Yellowstone.
This one from a small pot in the Bijah Group (no. 118) was at 25° C.,
growing on the moist vertical walls of the spring. The material is sparse
but quite distinctive.

7. Chroococcus endophyticus, sp. nov.

Plants endophytic in the strata of gelatinous Myxophyceae. Cells few to a
few hundred, in spherical to irregular often formless colonies; colonies up to
45μ in diameter; surface membrane of colony poorly defined. Cells spherical,
pale blue-green, without sheaths 1.3–2.0μ in diameter, with sheaths 2.1–3.0μ
in diameter. Individual sheaths mostly confluent with the colonial matrix,
homogeneous, not lamellate, hyaline, and almost invisible.

Chroococcus endophyticus resembles *C. limneticus* Lemm. in miniature. Its much smaller cell size, endophytic habitat, and more formless colonies make it quite distinct from the larger planktonic *C. limneticus* in spite of the resemblance. The frequent irregular form of the colonies is evidently correlated with the cramped position they occupy in the interior of the thallus of the plants in which they occur.

I have found *C. endophyticus* only in Bijou Geyser, Upper Geyser Basin (type: no. 439) at temperatures of from 32–49° C. and at a pH. of about 8.85–9.0. In this site it was quite common in the older portions of the strata of *Phormidium vesiculiferum* (of this paper), *Phormidium truncatum* var. *thermale* (of this paper), and *Mastigocladus laminosus* Cohn. It was most abundant in "algal stalactites" hanging from a sinter ledge, and receiving a steady supply of water with a temperature of 36.8° C. and a pH. of 8.95.
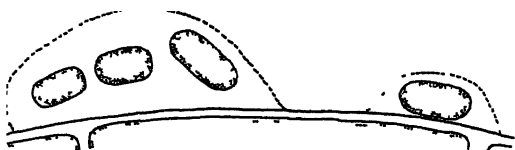
Fig. 10.—*Rhabdoderma zygnemicola,* on filament of *Zygnema* (×2060).

RHABDODERMA Schmidle et Lauterborn

in Schmidle, Beitr. Kennt. Planktonalg., Ber. deutch.

Bot. Ges. 18, p. 149, 1900.

Cells ovoid to cylindrical with rounded ends, straight, curved, or twisted; in colonies of a few in a homogeneous, difficultly visible matrix. Colonies spherical, flattened, or irregular. Cells single or following division in twos or short chains. Cell division transverse.

Type species: *Rhabdoderma lineare* Schmidle et Lauterborn.

The majority of species of *Rhabdoderma* are planktonic. Heretofore there have been no thermal species known. None have been previously credited to North America.

A single Yellowstone species.

1. **Rhabdoderma zygnemicola,** sp. nov.

Colonies minute, 1–few celled (mostly 1–4, rarely up to 10 or 11); hemispherical or flattened; epiphytic. Cells ovoid to short cylindric, straight; 1.9–2.4μ in diameter by 3.0–5.5μ in length, single or in pairs, with clear bright blue-green, homogeneous contents. Matrix homogeneous, hyaline, invisible without staining.

Occurring on *Zygnema,* and possibly other algae in thermal waters, *R. zygnemicola* can be immediately separated from the other species of *Rhabdoderma,* which are largely planktonic. In diameter this species roughly approximates *R. irregulare* (Neumann) Geitler; from it it differs in having much bulkier cells which are straight rather than "S" shaped.

In the Yellowstone Park *R. zygnemicola* is confined to sharply acid waters (below pH. 6.0). The type (no. 70) was collected in the Crater Hills near a small mud pot on wet mud and sinter, growing on *Zygnema* at 32.9°–43.8° C. and pH. 5.2. It was observed in a few other collections from the Crater Hills. In the springs of this locality the high concentration of alum and feeble flow of water were important factors in limiting the variety of algae. *Pluto caldarius* (Tilden) was the only other blue-green observed in most of the springs of the entire group.

COELOSPHAERIUM Naegeli

Gattungen einzelliger Algen, p. 54, 1849.

Cells spherical, elliptical or egg-shaped, during division often "heart-shaped," united into unattached, spherical colonies, with the cells arranged around the periphery, and with or without distinct special sheaths; colonial matrix often radially fibrillar. Cell division in two planes, at right angles to each other and parallel to a radius of the colony passing through the dividing cell. Cell contents without or usually with pseudovacuoles. Multiplication through fragmentation of the colony into two or more parts, or less often through the release of single cells.

The majority of the several species are planktonic in lakes, ponds, and sluggish streams; a few are found in brackish water and one is marine. There are no previous records of thermal habitats.

A single Yellowstone species.

1. COELOSPHAERIUM MINUTISSIMUM Lemmermann

Ber. deutsch. Bot. Ges., p. 98, 1900.

Colonies spherical or ovoid, 20–30μ in diameter, with a thin colonial tegument. Cells spherical, 1μ in diameter, pale blue-green, pseudovacuoles absent.

The species is known from fresh, polluted, and brackish waters. It is usually planktonic. Its previously reported occurrences included neither warm waters nor American localities.

In the Yellowstone the species has been found a single time. It was occasional to rare in a small pot in the Bijah Group (no. 118), growing at 25° C. In this site it occurred among other Myxophyceae as a component of the surface crust of algae that entirely covered the pool.

ANACYSTIS Meneghini

Conspectus algologiae Euganeae. 1837.

Syn.: *Microcystis* Kützing, Linnaea 8, p. 372, 1833, pro parte.
Gloeocapsa Kützing, Phyc. gen., p. 174, 1843, pro parte.

Cells spherical to elliptical or subcylindrical, united into more or less spherical colonies of at maturity many cells, and of definite form. Colonial tegument homogeneous or often lamellate, usually with a firm distinct outer membrane; cells with or without individual special sheaths, matrix usually hyaline. Cell contents usually blue-green, less often violet or steel-blue; pseudovacuoles present or absent. Cell division in two or three planes in the spherical-celled species; transverse in the elongate-celled species. Multiplication through the encystment of the cells of the colony and the release of the gonidia.

Anacystis has been regarded by most recent authors as a partial synonym of both *Microcystis* and *Gloeocapsa*. Until recently there has been little emphasis on the modes of reproduction and life cycles of the Chroococcaceae. I am following Gardner (1927) in recognizing the genus as valid. As has been clearly stated by him, the distinctive method of multiplication in *Anacystis*, with gonidia with thickened and elaborate membranes is almost unique, and the regular disintegration of the parent colony after their formation is not found in other Chroococcaceous genera, esp. *Microcystis* and *Gloeocapsa*. Resting cells occur in other genera but are not the chief agents of multiplication; rather they are resting structures that carry the plant through dormant periods.

The species of *Anacystis* are found mostly on damp soil, rocks, etc., and less often in fresh water, sometimes planktonic. There is a single recorded thermal species: *A. minutissima* Gardner, known from damp rocks and the overflow from a Hot Spring in Porto Rico.

A single Yellowstone species.

1. Anacystis thermalis, sp. nov.

Cells ovoid, 3.0–3.5μ in diameter by 3–6μ in length, united into spherical or subspherical colonies of many cells and up to 70μ in diameter; cells loosely placed in young colonies, closely packed in older ones. Colonial tegument broad, hyaline and difficultly visible, and feebly lamellate; individual sheaths completely confluent and not visible. Cell contents blue-green to violet, mostly with a prominent granule. Gonidia short ovoid, 3.5–3.7μ in diameter by 3.8–4.0μ in length, with a purplish, transparent membrane.

This species is quite distinct from the previously described members of the genus. The characteristic morphology, color, and habitat all enable the plant to be recognized immediately.

The only collection in which *A. thermalis* was found was from a spring at the source of Fairy Creek, Twin Buttes Region (type, no. 413), where it occurred in abundance at 42° C. and pH. 8.1, mixed with *Oscillatoria princeps tenella* (of this paper), *O. terebriformis* (Ag.) Gom., *Phormidium tenue* (Mcne.) Gom., *P. valderianum* (Delph.) Gomont, *Spirulina caldaria* Tilden, *S. caldaria magnifica* (of this paper), *Myxosarcina*
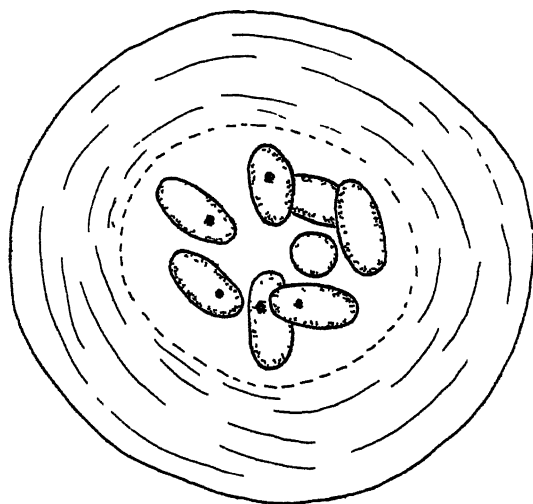
Fig. 11 —*Anacystis thermalis,* small colony
(×1700).

amethystina (of this paper), and *Chroococcus tenacoides* (of this paper). The algal mass formed a dark bluish-black to steel-blue floating stratum 3–10 cm. thick that filled the spring pool. No data were collected on the temperature range of the organism and it is impossible to make any deductions as to its occurrence, other than that it is quite local.

SYNECHOCYSTIS Sauvageau

Algues recolt. en Algérie, Bull. soc. Bot. France 39, p. 71, 1892.

Cells spherical, following division hemispherical, solitary or following division in twos, without visible sheaths.

Type species: *Synechocystis aquatilis* Sauvageau.

The several species of the genus differ widely in habitats. They vary from fresh water pools and streams to mineral springs, brackish and

salt waters, salinas, and moist rocks. The type species, *S. aquatilis,* has been found in a warm stream in Algeria.

In the Yellowstone the genus is not important.

<center>KEY TO THE YELLOWSTONE SPECIES.</center>

I. Cells 1.5–1.8μ in diameter.   *S. thermalis* 1.
II. Cells 2.0–2.4μ in diameter.   *S. minuscula* 2.

<center>1. **Synechocystis thermalis**, sp. nov.</center>

Cells spherical, 1.5–1.8μ in diameter, solitary, following division hemispherical and in pairs. Cell contents homogeneous, blue-green.
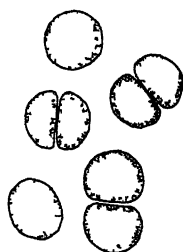
<center>FIG. 12.—*Synechocystis
thermalis* (×4410).</center>

This is one of the smaller species of the genus. Its average size is less by 0.5μ than that of *S. minuscula* Woronichin, and larger by 0.7μ than *S. primigenia* Gardner, the only smaller species known.

The species is known from a single locality: one of the Meadow Springs about one-half mile north of Semicentennial Geyser. When collected, it was growing at a temperature of 62.2° C. and a pH. of 5.4. In this site it was quite abundant (type: no. 193), growing with and among various species of *Synechococcus.*

<center>2. SYNECHOCYSTIS MINUSCULA Woronichin</center>

<center>Biol. Seen Pjatigorisk, Arch. Hydrobiol. 17, p. 642, 1928.</center>

Cells spherical, 2.0–2.4μ in diameter, solitary or following division hemispherical and in pairs, with a very thin hyaline tegument, blue-green. Cell contents homogeneous.

Described from a bitter mineral spring in the northern Caucasus, this species has not been otherwise noted.

In the Yellowstone it has been found in the bottom (algal) crust of Firehole Lake in the lower Geyser Basin (no. 400), at 36° C. and pH.

8.3. It was among *Phormidium laminosum* (Ag.) Gom., *Synechococcus Minervae* (of this paper), *Aphanothece saxicola* Neag., and incidental forms, in small quantities.

SYNECHOCOCCUS Naegeli

Gattungen einzelliger Algen, p. 56, 1849.

Cells ellipsoidal to cylindrical, with rounded ends, straight or curved, single or in twos, less often in fours; tegument none or very thin and almost invisible; division transverse; cells often motile.

The species of *Synechococcus* are known from a variety of habitats: salt water, fresh water, and damp soil. *S. curtus* Setchell was described from hot salt water. *S. aeruginosus* Naeg. has been reported from thermal waters in the Yellowstone by Tilden (1897). On the whole the genus has been considered as a distinctly non-thermal group of species.

In the Yellowstone, *Synechococcus* is one of the most abundant and characteristic genera of the thermal Myxophyceae. It is one of the four which occur at temperatures as high as 80° C. and is notable as well for its widespread occurrence. Species of the genus have been found in at least 70% of all the collections of algae I have from the Yellowstone.

KEY TO THE YELLOWSTONE SPECIES

I. Cells elliptical to subcylindrical.
  1. Cells less than 3μ in diameter.
    A. Cell contents homogeneous, blue-green.   *S. eximius* 1.
    B. Cell contents with at least several granules, pinkish to rose red.
                                    S. roseus 2.
  2. Cells greater than 3μ in diameter.
    A. Cell contents violet.   *S. amethystinus* 3.
    B. Cell contents blue-green, or at least not violet.
      a. Cells 3–6μ in diameter.
        *. Cell contents with rows of granules.   *S. Minervae* 4.
       **. Cell contents with scattered granules or none.
          !. Division always transverse.
                        S. Minervae var. *maior* 4A.
         !!. Division sometimes longitudinal.
                      S. Minervae var. *bigeminatus* 4B.
      b. Cells 7–16μ in diameter.   *S. aeruginosus* 5.
II. Cells cylindrical, straight or curved.
  1. Cell contents mostly with a few prominent granules.
    A. Granules polar or usually polar.
      a. Cells distinctly curved.   *S. vescus* 6.
      b. Cells more or less straight
        *. Cells less than 1.7μ in diameter.   *S. lividus* 7.

**. Cells greater than 1.7μ in diameter.

          S. elongatus var. *amphigranulatus* 8A.

 B. Granules variable in position, not regularly polar.

  a. Cells straight or slightly curved.   *S. viridissimus* 9.

  b. Cells distinctly curved or bent.

    *. Cells evenly and distinctly curved.

          S. lividus var. *curvatus* 7A.

  *+. Cells obtusely bent.   *S. lividus* var. *siderophilus* 7B.

2. Cell contents without granules, homogeneous.

 A. Cells before division more than 13μ in length.

  a. Cells less than 2.5μ in diameter.   *S. Vulcanus* 10.

  b. Cells greater than 2.5μ in diameter.

        S. Vulcanus var. *bacillarioides* 10A.

 B. Cells before division less than 13μ in length.

  a. Cells strongly curved.   *S. arcuatus* 11.

  b. Cells straight or feebly curved.

    *. Cells 2μ or less in diameter.   *S. elongatus* 8.

    **. Cells 2μ or greater in diameter.

         S. elongatus var. *vestitus* 8B.
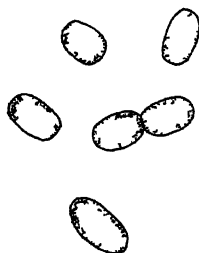
FIG. 13.—*Synechococcus eximius* (×2020.)

FIG. 14.—*Synechococcus roseus* (×2750).

1. Synechococcus eximius, sp. nov.

Cells ovoid to subcylindrical, pale blue-green, with homogeneous contents, 1.8–2.5μ in diameter by 1.2–2.0 diameters in length, 2.2–3.5μ long; cells single or during division in twos.

Although close in size to *S. elongatus* Naeg., this species may be distinguished from it by its broader and shorter cells. The more homogeneous cell contents and grayish shade of blue-green in *S. eximius* likewise aid in separating the two.

S. eximius is distinctly a limital thermal species. The type (no. 73), from wet rocks in steam vent near the Giant Sulphur Spring, Crater Hills, grew at a temperature of 80.2° C. and a pH. of 4.6. The water, although acid, had little dissolved salts in it and was much less poisonous than most of the springs in the Crater Hills. This species was not found

outside the single set of springs, although it is probably to be discovered in others, such as the Monument Geyser Sulphur Springs and Roaring Mountain Springs. The temperature range in which it has been found extends from 68° C. to 83.6° C. The acidity was in every case pronounced, pH. 4.5–5.3.

2. Synechococcus roseus, sp nov.

Cells ellipsoidal, 1.8–2.1μ in diameter by 1.5–2.5 diameters in length, 3–5μ long, single or following division in pairs, pale pink to clear pinkish rose in color; without sheaths or matrix. Cells often in irregular clumps and sometimes forming pink botryoidal masses up to 1 mm. thick. Cell contents granular.

The pink color, as well as the characteristic morphology, sets this species apart from the other members of the genus.

S. roseus is known only from a pool in the White Elephant Grottoes, Mammoth Hot Springs. There it was locally subdominant, covering a stratum of *Phormidium* and growing among *Beggiatoa* in a shallow pool near a spring vent (type: no. 90) at 49° C. and pH. 7.1. It was associated with *Spirulina labyrinthiformis* Menegh., *Phormidium laminosum* (Ag.) Gom., *P. purpurascens* var. *laminatum* (of this paper), *Oscillatoria amphibia* Ag. and *Synechococcus Minervae* (of this paper), as well as sulphur bacteria.

3. Synechococcus amethystinus, sp. nov.

Plants unicellular, often in pairs following division; cells subcylindrical, naked, violet in color, 3.2–3.6μ in diameter by 1.5–2.5 diameters in length, 4–9μ long. Plant mass dull violet, mostly poorly defined, flocculent, or more frequently endophytic in gelatinous algae. Cells separating promptly after division. Cell contents homogeneous or often with one large granule of irregular position.

Occurring mostly on or in the strata of species of *Phormidium,* this species of *Synechococcus* is quite unmistakable. It approaches closely in certain respects both *S. Minervae* (of this paper) and *S. Cedrorum* Sauvageau. From both it is to be separated by the more homogeneous protoplasm (aside from the granule which often is present) and the distinctive color. Its habit of growth—frequently deeply imbedded—is unusual; and its size is slightly smaller than *S. Cedrorum,* and its length proportionally greater than *S. Minervae.* The color of the alga changes gradually in formalin-preserved material and after a few weeks it assumes almost a rose color. When kept in the dark, the violet is retained indefinitely.

S. amethystinus, as far as it has been found, is confined to the Twin Buttes Region, especially to the stream carrying the runoff water from

Spray Geyser and the now non-eruptive Imperial Geyser. It has been found in water of 42–55° C., and from pH. 8.85 to 8.95. The type (no. 417) was at 47.2° C. and pH. 8.9, growing in *Phormidium laminosum* (Ag.) Gom. in shallow water.

4. Synechococcus Minervae, sp. nov.

Cells single or following division, in pairs, elliptical, naked, pale blue-green in color, 3–3.6μ in diameter by 1.5–2.0 diameters in length, 4.5–7.0μ long. Plant mass olive-green to dull blue-green, soft, thin, and flocculent; or cells scattered on or among other algae. Division transverse, cells separating promptly after division; pairs frequent but always separating before the next division. Cell contents blue-green, with longitudinal rows of fine granules.

S. Minervae is close to *S. Cedrorum* Sauvageau. While the differences between the two are slight, they are easily distinguished. *S. Minervae* is more gibbous, and is distinctly shorter, not exceeding 7μ in length. *S. Cedrorum* is typically subcylindrical, less often cylindrical or nearly so, and is usually longer, often up to 10μ in length. *S. Cedrorum* is much brighter in color while *S. Minervae* is paler and often rather olive-green. In temperature relations the species are totally different: *S. Cedrorum* (in pure cultures) having an optimum between 20° and 30° C.; *S. Minervae* (in pure cultures) having an optimum above 55° C.

This species is one of the most abundant and characteristic forms of the Mammoth Hot Springs. It occurs most frequently mixed with other algae: species of *Phormidium, Spirulina labyrinthiformis* Menegh., *Synechococcus lividus* (of this paper), and others; rarely it grows alone or as a dominant form. The species has been named because of its noteworthy abundance at Minerva Terrace, Mammoth Hot Springs, over a period of at least four years. The springs at Mammoth in which it has been noted include in addition to Minerva Terrace: Orange Spring Mound (no. 88), Orange Spring Mound, Jr. (nos. 77, 78, 79, 80, 81, 82, 83, 86, 87), White Elephant Grottoes (nos. 89, 97, 99, 100), Angel Terrace (no. 158), Jupiter Terrace, Diana Terrace, Main Terrace, Hymen Terrace, Cleopatra Terrace, Narrow Gauge Terrace, White Elephant Terrace, Stygian Caves, and the small marsh below Jupiter Terrace. Outside of the Mammoth Hot Springs it is frequent. It is known from the Boiling River Group: Riverside Cone; Bijah Group: Bijah Spring Pool (no. 132); and Twin Buttes Region: Spray Geyser overflow (no. 426). It has not been found in the major Geyser Basins. Its temperature range as observed is 23.5°–64.1° C.; its pH. range from 6.45 to 8.95. The type (no. 78, Orange Spring Mound, Jr., almost pure) was growing

at 57° C. and pH. 6.8. The species is typically thermal and is abundant only above 40° C. and below pH. 7.8.

4A. SYNECHOCOCCUS MINERVAE

var. maior, var. nov.

Cells 3.6–4.2μ in diameter by 1.5–2.0 diameters in length. Cell contents with 1-6 prominent granules; without granular rows. Plant mass bright blue-green. Otherwise as in the species.

The variety *maior* differs from *S. Minervae* only in slight ways. The difference in size is constant and very few cells of the species are as large as the smallest of the variety. The two forms are both quite constant in nature and also in pure culture. The clear blue-green mass formed by the variety *maior* is distinct from the duller mass of *S. Minervae*.

S. Minervae var. *maior* occurs chiefly as an incidental or occasional form among other Myxophyceae or on various algae, especially species of *Phormidium*. It is found generally throughout the Yellowstone except in acid waters and in highly calcareous springs. Its known distribution includes Twin Buttes Region: Spray Geyser (nos. 424, 425, 427, 428, 429); Imperial Geyser overflow (nos. 414, 415, 416); Upper Geyser Basin: Handkerchief Pool (no. 351); Lower Geyser Basin: several springs; Bijah Group; Elk Park; and several isolated springs. The type (no. 210) is from Elk Park, growing in a small unnamed spring in the northeast part of the valley, at 47° C. and pH. 8.05. The temperature and acidity range noted for the plant is from 31° to 56.6° C., from pH. 6.10 to 9.05.

4B. SYNECHOCOCCUS MINERVAE

var. bigeminatus, var. nov.

Cells 3.4–4.0μ in diameter by 1.2–1.6 diameters in length. Cells scattered among other algae. Division usually transverse, occasionally longitudinal. Cells separating late after division; single cells occasional, pairs numerous and groups of four not infrequent. The groups of four are either in the form of linear chains or plates. Otherwise as in the species.

While *S. Minervae* var. *bigeminatus* differs from *S. Minervae* slightly in size and shape, their behavior during and after fission is more characteristic. The larger proportion of paired cells in the variety is quite striking and the occasional groups of four are completely distinctive. The platelets of four cells are formed by successive divisions at right angles to each other. Their formation in a species of *Synechococcus* is anomalous and the retention of this form in the genus would be ques-

tionable if it were not for its very close similarity to *S. Minervae* and *S. Cedrorum* Sauv. On the other hand, the chains of four cells, somewhat more numerous than the platelets, are formed in the normal manner, by transverse division.
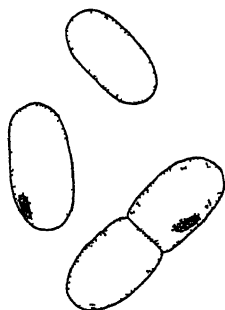
FIG. 15.—*Synechococcus amethystinus* (×2650).
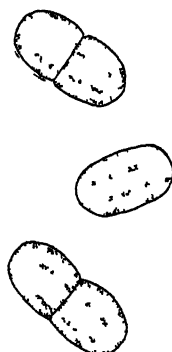
FIG. 16.—*Synechococcus Minervae* (×2420).
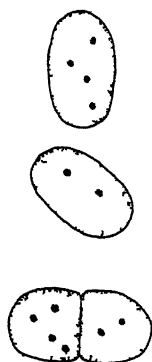
FIG. 17.—*Synechococcus Minervae* var. *maior* (×2420).

FIG. 18 —*Synechococcus Minervae* var. *bigeminatus* (×2420).

This variety has been found only in the Chocolate Pots (Iron Springs) of the Gibbon Valley (nos. 273, 274, 275, 277). The type (no. 277) was growing at 51° C., pH. 7.0. It was associated with *Synechococcus lividus* var. *siderophilus* (of this paper), the two growing on and in an encrusted precipitate of iron compounds.

5. Synechococcus aeruginosus Naegeli

Gattungen einzelliger Algen, p. 56, 1849.

Cells ellipsoidal to short-cylindrical, 7–16μ in diameter by 2 diameters in length, mostly single or following division in pairs, bright to pale blue-green, rarely golden; ends broadly rounded. Cell contents often with numerous peripheral granules.

The species seems to exist as two possibly distinct forms; the systematic relationship of the two is not clear.

Tilden (1896, 1897, 1898) reported the occurrence of *S. aeruginosus* in a thermal situation in the Yellowstone. The material on which she based her report was collected in 1896 in a small cave by a geyser cone in the Nez Perces Valley, Lower Geyser Basin. She found it as a component of "algal stalactites"; the accompanying algae she reported to be *Phormidium purpurascens* (Kütz.) Gom. and *Gloeocapsa violacea* (Corda) Rabenhorst. Later Tilden (1910) states that the *P. purpurascens* "should be placed under *Hypheothrix calcicola* (Ag.) Rab." The record of *P. purpurascens,* nevertheless, she believed should be allowed to stand "since there is some possibility that the material contains a mixture of the two species." The *G. violacea* (Corda) Rabenhorst I find to have been *G. compacta* Kütz. It seems doubtful to me that *S. aeruginosus* Naeg. really occurs in the Yellowstone thermal waters. At least, with several hundred collections of material I have not come upon it, and there is only the above record in its favor. However, the species is to be found in non-thermal waters in the Park. It has been noted on three occasions in the vicinity of the Mammoth Hot Springs, on wet and dripping rocks.

6. Synechococcus vescus, sp. nov.

Plants unicellular, solitary or in pairs, epiphytic on gelatinous algae. Cells slender, cylindrical, evenly curved to at most an arc of ⅙ of a circle, or occasionally almost straight (curved in one plane—not twisted), 1.8–2.1μ in diameter by 8–26μ (mostly 10–20) long, 7–22μ across the arc formed by the bent cell. Cell content clear blue-green, more deeply pigmented at periphery, and with polar granules single or in unequal pairs. Polar granules variable in shape and size, usually large and highly refractile, when pairs are present the terminal one larger. Plant mass clear blue-green, very soft, flocculent.

S. vescus falls in the same group with *S. Vulcanus* (of this paper), *S. Vulcanus* var. *bacillarioides* (of this paper), and *S. arcuatus* (of this paper). From all of these it may be separated by its greater length, its proportionally more slender cells, and by its polar granulation. The frequent unequal paired polar granules seem to separate it from all other

species of *Synechococcus*. Under the microscope it is one of the most easily recognized species of the genus.

Probably *S. vescus* occurs throughout the Yellowstone Hot Springs except for those with extremely acid water. It reaches its greatest abundance in hot, basic waters and there may form an almost pure sediment on the bottom of shallow sluggish pools or rills. It has been found in the following sites: Upper Geyser Basin: Emerald Pool (no. 353), Chromatic Spring; Midway Geyser Basin: Excelsior Geyser Crater (no. 358); Lower Geyser Basin: Great Fountain Geyser runoff; Twin Buttes Region: Spray Geyser (no. 426), Spray and Imperial Creek (no. 414); Elk Park: small spring (nos. 215, 216, 217); Meadow Springs (no. 190); Chocolate Pots (no. 273); and Mammoth Hot Springs: Main Terrace (no. 229). The type (no. 210, Elk Park) was growing at 47° C. and pH. 8.05.

7. Synechococcus lividus, sp. nov.

Cells cylindrical, usually straight or sometimes feebly curved, 1.2–1.4μ in diameter by 5–10μ in length, separating soon after division, but frequently in linear pairs. Plant mass flocculent, livid blue-green. Cell contents usually with one or two granules, polar in position, sometimes absent; olive-green to dull blue-green.

Although quite distinct from most of the species of *Synechococcus, S. lividus* is close to certain other species, especially *S. elongatus* Naegeli and *S. viridissimus* (of this paper). From *S. elongatus* it differs in its more slender form and in possessing a distinctive granulation; from *S. viridissimus,* in its more slender cells and definite granule arrangement.

In the Mammoth Hot Springs the species is widespread and abundant; elsewhere it is rare or occasional. The springs at Mammoth in which it has been found include: Orange Spring Mound, Jr. (nos. 77, 78, 79, 80, 81, 82, 86, 87); White Elephant Grottoes (no. 99); Angel Terrace (no. 158); Diana Terrace (no. 201); Blue Pool Terrace (nos. 221, 227); Main Terrace (no. 229); The Esplanade; Orange Spring Mound; Minerva Terrace; Jupiter Terrace; Cleopatra Terrace; Hymen Terrace; Narrow Gauge Terrace; Mound Terrace; and the Mammoth Swimming Pool. Outside of the Mammoth Group it has been found in the Boiling River Group: Riverside Cone (no. 272); Bijah Group: surface of small pool (no. 122); Twin Buttes Region: Imperial Geyser (no. 326); and the Upper Geyser Basin: Handkerchief Pool (no. 351). The known range of the plant includes temperatures from 23.5° C. to 68° C., acidities from pH. 6.1–8.8. Its greatest abundance has been found to be slightly on the acid side of neutral and between 50° and 65° C. The

type (no. 77, Orange Spring Mound, Jr.) was growing at 59° C. and pH. 6.5, and along with *S. Minervae* (of this paper) was a co-dominant form. The total number of collections in which this species was found is well in excess of one hundred. In general it accompanied other Myxophyceae, such as *Phormidium, Synechococcus,* and *Oscillatoria.*
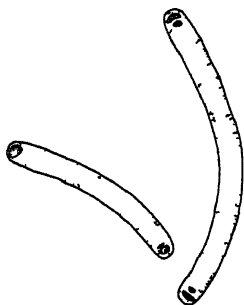
FIG 19.—*Synechococcus vescus* (×1500).
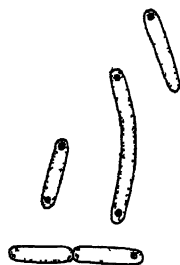
FIG 20.—*Synechococcus lividus* (×1370).

FIG. 21 —*Synechococcus lividus* var. *curvatus* (×1370).
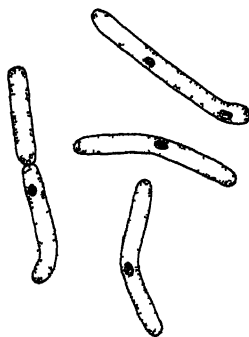
FIG 22.—*Synechococcus lividus* var. *siderophilus* (×1370).

7A. SYNECHOCOCCUS LIVIDUS

var. curvatus, var. nov.

Cells cylindrical, 1.7–2.2μ in diameter by 6–13μ in length. Cell contents pale blue-green, with usually one or two granules that are not definite in position. Cells uniformly and distinctly curved for their entire length, or less often almost straight. Cells separating immediately after division so that pairs of cells are rarely found

The variety *curvatus* differs from *S. lividus* by its larger size, variable granulation, and regular curvature. It is notable that the slight but constant difference in speed of separation following division is constant over a wide temperature range in both *S. lividus* and the variety *curvatus;* there being no deviation in *S. lividus* between 23.5° C. and 68° C.; in the variety *curvatus,* none between 38° C. and 68° C.

Occurring only in the basic, silicious springs, this variety is locally quite important. Its range includes the Upper Geyser Basin (various springs and in the Firehole River) (nos. 440, 441, 442) ; Lower Geyser Basin; Twin Buttes Region: Spray Geyser (nos. 417, 423) ; West Thumb (no. 447). The type (no. 447) is from the largest spring at West Thumb, where it occurred on a stratum of *Phormidium laminosum* (Ag.) Gom., at 52° C. and pH. 8.6. This variety has been found at from 38° to 68° C., at from pH. 8.6 to 9.0.

7B. SYNECHOCOCCUS LIVIDUS

var. siderophilus, var. nov.

Cells cylindrical, 1.5–1.8μ in diameter by 8–15μ in length. Cell contents pale blue-green; mostly with one or two granules of indefinite position. Cells separating very soon after division and pairs rarely found. Cells straight, or mostly obtusely bent.

S. lividus var. *siderophilus* is close to *S. lividus*. It differs from it by its larger size, less definite position of granules, more prompt separation of daughter cells, and by its often characteristically bent cells. Single specimens of the species and variety might in many cases be indistinguishable. With several specimens of each the separation is, nevertheless, sharp.

The variety *siderophilus* is named because of its very characteristic occurrence in the Iron Springs (Chocolate Pots) of the Gibbon Valley. The type (no. 277) is from the largest of these springs, on the east bank of the river. The type was growing at a temperature of 51° C. and a pH. of 7.0, with *Synechococcus Minervae* (of this paper), in and among a granular and encrusted deposit of iron salts, the whole having a very dark rusty brown color. The variety has been found at temperatures ranging from 43° to 59° C. and at acidities from pH. 6.7 to 7.4.

8. SYNECHOCOCCUS ELONGATUS Naegeli

Gattungen einzelliger Algen, p. 56, 1849.

Syn.: *Synechococcus parvulus* Naegeli, Gatt. einzell. Algen, p. 56, 1849.
       Synechococcus racemosus Wolle, Bull. Torr. Bot. Club 8, p. 37, 1881.

Cells cylindrical, straight, 1.4–2.0µ in diameter by 1.5–3.0 diameters in length, 2–6µ long, single or in chains of 2–4; cell contents pale blue-green and homogeneous or finely granular.

S. elongatus has been studied in pure culture by various workers. While constant under normal conditions for growth, involutions have been observed in old dry cultures. The abnormal features presented by these involution forms were chiefly in part a greater length, irregular curvature of the cells, and asymmetric (unequal) fission. Such abnormal cells, while striking in appearance, should be easily recognized for what they are.

In the Yellowstone the species is present in non-thermal sites in its usual place: moist earth, edges of pools, wet cliffs, etc. The only locality in which its range included even a semi-thermal temperature was at Mammoth Hot Springs in the Stygian Caves (no. 145). There it grew on the damp shaded roof of a small grotto at 14° C. and pH. 8.1. The plant is apparently strictly non-thermal.
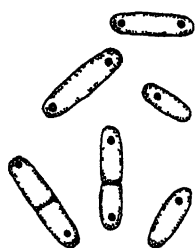
FIG. 23.—*Synechococcus elongatus* var. *amphigranulatus* (×1250)

FIG. 24.—*Synechococcus elongatus* var. *vestitus* (×1360).

8A. SYNECHOCOCCUS ELONGATUS Naegeli

var. amphigranulatus, var. nov.

Cells straight or lightly curved, 2.0–2.9µ in diameter by 1.5–3.0 diameters in length, 4.4–9.0µ long; plant mass flocculent, arsenic-green, or scattered singly among other algae; cell contents bright blue-green, with 1–2 (rarely more) prominent polar granules, mostly two in mature cells and one in cells just after fission. Otherwise as in the species.

This variety differs from the species quite sharply and might be considered as a separate species.

Although widely distributed in the Yellowstone, this form was not frequently met with in abundance. It has been found in the Meadow Springs (nos. 187 and 193); Elk Park: large spring (no. 217); and

Twin Buttes Region: Spray Geyser (nos. 424, 427, and 428). The type (no. 187) was at 48° C. and pH. 6.65. The extremes of temperature and acidity as observed were 33.1° C. and 63° C.; pH. 5.4 and 9.0. It will be noted that the variety is clearly distinct from *S. elongatus* in thermal distribution.

8B. SYNECHOCOCCUS ELONGATUS Naegeli

var. vestitus, var. nov.

Stratum clear, light blue-green, up to 1 mm. in thickness, usually flocculent to fibrous (due to included lime), composed of naked cells held together with dendritic calcium-carbonate crystals; surface of stratum often clothed with a fine fragile woolly layer of crystals, sometimes cells scattered among other algae; cells cylindrical, straight, 2.0–2.4μ in diameter by 2–4 diameters in length, 4–9μ long. Cell contents homogeneous, without prominent granules.

While close to the species microscopically, the larger size and proportionally greater length are distinctive. The elaborate and striking plant mass is unique among species of *Synechococcus*. Undoubtedly the clothing and binding action of the calcium carbonate crystals is largely the cause of the often firm texture. Further study is needed to determine the constancy of the gross characteristics.

The localities for the species as noted in this study are:— Mammoth Hot Springs: Sunken Spring (type: no. 141); Bijah Group: small pot (nos. 119 and 122); Artist's Paintpots (no. 298); Elk Meadow: large spring (no. 215); Meadow Springs (no. 185); and Twin Buttes Region (no. 418). It is notable that none of these springs are lime-depositing and contain in general only small traces of calcium carbonate (the Sunken Spring is one of the few at Mammoth with little lime and no appreciable deposition). The type (no. 141) was at 52° C. and pH. 6.35. The species ranges from 37.4° to 64.6° C., and from pH. 6.1 to 8.95. Its optima are near 54° C. and pH. 6.6.

9. Synechococcus viridissimus, sp. nov.

Cells cylindrical, straight or occasionally feebly curved, 2.0–2.5μ in diameter by 2–4 diameters in length, 4–11μ long. Cells usually scattered among other algae, less often forming a flocculent blue-green indefinite mass. Cell contents light blue-green, usually with 1 (0–3) small, conspicuous, flattened refractile granule, closely appressed to the cell wall, and indefinite in position. Cells single or following division, in pairs.

S. viridissimus differs from certain other species of *Synechococcus* by technical but sharp characters. From *S. lividus* (of this paper) it may be separated by its more bulky form, its appressed, non-polar granulates, and

it., greater size; from *S. elongatus,* by its larger size, more elongate form and its granulation.

This species is quite abundant in the strongly basic waters of the Geyser Basins, and occurs widely in neutral or feebly acid waters as well. The type (no. 442) is from the Firehole River at the point of entrance of the overflow from Bijou Geyser and a small hot spring, growing at 55° C. and pH. 8.55. In this rather typical site, it was growing on and among other Myxophyceae: species of *Oscillatoria, Phormidium, Masti-gocladus, Symploca,* etc., covering them with a thick flocculent layer that partially or completely altered their normal appearance. It has been noted in the following localities:—Upper Geyser Basin: Emerald Pool (no. 353); Bijou Geyser (nos. 434, 437); Spring on Bijou Cone (nos. 440, 441); Rainbow Pool; Sunset Lake; Green Spring; Punch Bowl Spring; Chromatic Pool; Beauty Pool; Wave Spring; Beach Spring; and others; Midway Basin: Grand Prismatic Spring; Excelsior Geyser Crater; Lower Geyser Basin: Tank Spring; Jelly Spring; and others; Twin Buttes Region: Spray Geyser (nos. 310, 421, 422, 423); Artist's Paintpots (no. 298); Meadow Springs (nos. 185, 188, 190, 193); and elsewhere. The temperature range for the species has been observed to be from 42° to 69.5° C.; the acidity range from pH. 5.4 to 9.0. The optima seem to be about 58° C. and pH. 8.4. The species is strictly thermal.

10. Synechococcus Vulcanus, sp. nov.

Cells cylindrical, straight or feebly curved, 2.1–2.4μ in diameter by 7–17μ in length. Cell contents homogeneous, pale yellowish-green. Cells among other algae or forming a poorly defined lemon-yellow flocculent stratum.

On the whole, this is one of the most distinct of the Yellowstone species of *Synechococcus.* Involution forms have been noted at temperatures above 82° C.

This species is the characteristic limital thermal form of the strongly basic springs of the Geyser Basins. The type (no. 324) is from the overflow of the Imperial Geyser Crater, Twin Buttes Region, where it formed at pure growth on the bottom of the creek at 71.1° C. and pH. 8.8. The typical lemon-yellow color was modified in this site by a mixture of silt with the algae. The species has been found in several springs, including the following:—Twin Buttes Region: Imperial Geyser Crater (nos. 322, 324, 327, 415); Spray Geyser (no. 353); Black Sand Pool; Punch Bowl Spring; Morning Glory Pool; and others; Midway Basin: Grand Prismatic Spring; Excelsior Geyser Crater; Lower Geyser Basin: Great Fountain Geyser; Elk Park: Large Spring (no. 214). Its range in tem-

perature and acidity has been observed to extend from 47.2° C. to 84° C., from pH. 8.6 to 8.9. Its optima are probably near 70° C. and pH. 8.8. It is notable that only two species of Myxophyceae have been recorded at higher temperatures than this one inhabits: *Phormidium bijahensis*

FIG 25 —*Synechococcus viridissimus* (×1650).
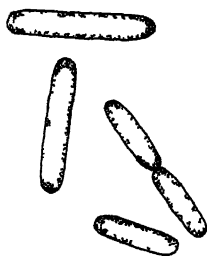
FIG 26.—*Synechococcus Vulcanus* (×1220)
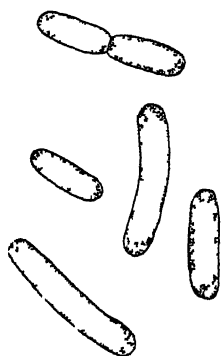
FIG. 27.—*Synechococcus Vulcanus* var. *bacillarioides* (×1390).

FIG 28 —*Synechococcus arcuatus* (×1840)

(of this paper), found up to 85.2° C., and *Oscillatoria filiformis* (of this paper), up to 85.2° C. One other species, *Phormidium geysericola* (of this paper), has been found at as high a temperature (84° C.). At the lower temperature range for the species it occurs as an incidental form, mixed with other Myxophyceae.

10A. SYNECHOCOCCUS VULCANUS

var. **bacillarioides,** var. nov.

Cells straight or usually feebly curved; 2.5–3.0μ in diameter by 7–16μ in length. Cell contents bright blue-green. Otherwise as in the species.

This variety is close to the species in morphology but distinct in distribution and gross appearance, and is much less common. The type (OS.28) is from Jupiter Terrace at the Mammoth Hot Springs; the other sites include: Midway Geyser Basin: Excelsior Geyser Crater overflow (nos. 357, 358); Bijah Group: Bijah Spring (nos. 132, 133). It has been found in waters at from 58° C. to 66.5° C., from pH. 7.1 to 8.3.

11. **Synechococcus arcuatus,** sp. nov.

Cells cylindrical, strongly and evenly curved, 1.5–2.0μ in diameter by 6–11μ in length, cells scattered among other algae or forming a loose flocculent gray-green to dull blue-green stratum. Cell contents homogeneous, without prominent granules, dull blue-green.

The even marked curvature of the cells gives this species a characteristic appearance not easily confused with the other species of *Synechococcus.*

It has been found in several sites that present a variety of conditions. The type (no. 132) is from Bijah Spring, where it occurred at 64.1°C. and pH. 7.95 as a co-dominant form. Other localities include: Upper Geyser Basin: spring near Grand Geyser (no. 391); Handkerchief Pool (no. 351); Twin Buttes Region: Spray Geyser (no. 423); Chocolate Pots (nos. 274, 275); and elsewhere. The species is met with usually as an epiphyte on larger Myxophyceae as species of *Oscillatoria, Phormidium, Symploca, Thalpophila,* etc. or as a flocculent precipitate on the bottoms of quiet pools. It inhabits water from 50° to 65° C., pH. 6.2 to 8.75. Its temperature range is apparently quite limited and it was noted in abundance only between 55° and 64.1° C.

DACTYLOCOCCOPSIS Hansgirg

Syn. gen. subgen. Myxoph., Notarisia 3, p. 590, 1888.

Cells cylindrical to ovoid or egg-shaped, pointed at one or both ends or tapering; straight, curved, bent or twisted, usually united into small colonies by an almost invisible matrix, or occasionally unicellular and without sheaths. Fission transverse.

Type species: *Dactylococcopsis rhaphidioides* Hansgirg.

The species of the genus live on moist soil, rocks, etc., or in standing

or slowly flowing water, often as plankton forms; brackish habitats are rare and marine have not been noted. *D. mucicola* Hustedt and *D. antarctica* F. E. Fritsch occur on and in the matrix of *Nostoc* spp. (and elsewhere). There are no previous records of the genus from thermal sources.

A single Yellowstone species.

1. DACTYLOCOCCOPSIS ANTARCTICA F. E. Fritsch

Freshwater Algae Nat. Ant. Exped., Nat. Hist. 6, p. 22, 1912.

Cells short spindle-shaped, often somewhat curved or slightly bent; apices acutely rounded but not sharp-pointed; 1.5–2.0μ in diameter by 4–6μ in length: cell contents pale blue-green, with one to a few small refractile granules.

Up to the present the only record for the species seems to be that of Fritsch (1912). He described the plant as growing on the surface of *Nostoc commune* Vauch., in the Antarctic. The presence of the species in the Yellowstone is surprising. The only site in which the organism was noted in the Park was at the edge of the rill from Spray Geyser at its junction with Imperial Creek, Twin Buttes Region (no. 429). There it was growing in small quantities on *Phormidium laminosum* (Ag.) Gom. and other gelatinous Myxophyceae at from 26° to 34°C. and at pH. 9.05.

It seems probable that the species is much more widely spread than the recorded data indicate and its occurrence in two such remote regions is less remarkable than it at first appears.

ENTOPHYSALIDACEAE Geitler

in Rabenhorst's Kryptogamen-flora XIV, p. 292, 1931.

Syn.: Entophysalidales Geitler, synop. Dar. Cyan., Beih. Bot. Centralbl. 41, pt. 2, 1925.

KEY TO THE YELLOWSTONE GENERA.

I. Plants filamentous.   HETEROHORMOGONIUM (p. 64)
II. Plants with a tubular sheath inclosing parallel placed, elongate cells or cell pairs, not filamentous.   BACILLOSIPHON (p. 66)

Heterohormogonium, gen. nov.

Plants free monosiphonous, branching filaments; cells imbedded in a gelatinous tegument, separate from each other and without intercellular protoplasmic strands. Branches originating by longitudinal division of one or a few intercalary cells and the subsequent splitting of a portion of the filament, eventually followed by the rupture of one or both sides of the loop thus formed; branching pseudodichotomous, often appearing lateral. Specialized cells

(heterocysts, spores, resting cells, etc.) absent. Hormogonia absent. Multiplication by fragmentation into shorter filaments, or by the discharge of single cells through dissolution or breaking of the tegument.

Type species: *Heterohormogonium schizodichotomum.*

The filaments bear a strong resemblance in their general structure to those of *Cyanothrix* Gardner. Unlike *Cyanothrix*, the branching and the liberation of single cells occur regularly in *Heterohormogonium.* Gardner (1927), in describing *Cyanothrix,* was handicapped by the scarcity of material. He suggested the probability of *Cyanothrix* freeing single cells in multiplication.

The systematic position of this genus as well as *Cyanothrix* is problematical. Gardner placed *Cyanothrix* in the Chroococcaceae, along with such genera as *Placoma* Schousboe and *Entophysalis* Kütz. He does not recognize the Entophysalidaceae as distinct from the Chroococcaceae. Geitler (1932) placed *Cyanothrix* tentatively in the Endonemataceae because of a resemblance to *Endonema* Pascher, and at the same time noted that it might be better placed in the Entophysalidaceae. The position of *Heterohormogonium* is rather more clear. The known lack of endospores tends to separate it from *Endonema,* and the fragmentation processes tend to ally it more closely with the Chroococcales. I am placing *Heterohormogonium* in the Entophysalidaceae and suggest that *Cyanothrix* might well belong in the same group. The growth habit and structure of *Lithococcus* Ercegovic (a member of this family) while much less sharply defined than that of either *Cyanothrix* or *Heterohormogonium,* is similar to them. Especially the clathrate, "branched" plant body is suggestive of the unique branching of *Heterohormogonium.*

A single species.

Heterohormogonium schizodichotomum, sp. nov.

Filaments scattered among other algae, pale arsenic green in color, flexuous to flexuously contorted, and somewhat entangled, around 2μ in diameter by up to cir. 1 mm. in length, mostly somewhat fragile and usually comparatively short; branching sparse. Branches frequently poorly developed and often forming merely short segments with a double row of cells, or short loops, but frequently long and free and appearing lateral or subdichotomous, similar to the main filament in size and structure. Tegument homogeneous, hyaline, firm, thin. Cells spherical to compressed spherical, distinctly separated, never crowded but often close or often distant; $1.2–1.6\mu$ in diameter by $1.0–2.5\mu$ in length, frequently in pairs flattened on adjacent sides; contents finely granular. Free cells spherical, $1.4–1.6\mu$ in diameter, naked, soon forming short sheathed filaments.

The only locality known for the plant is Soda Spring, Mammoth Hot Springs, where it was growing with diatoms, *Chara,* species of *Oscilla-*

toria, and purple bacteria at 28–42° C. and at pH. 6.5. The type (no. 127) was at 30° C. In this small spring the alga was quite common—a single drop of the ooze from the bottom usually having from 25 to 100 filaments. Soda Spring is a strongly mineral spring, that is at most lukewarm. Chemically and algologically it is distinct from the Mammoth Hot Springs formation. It may be described as a non-depositing, semi-thermal spring with calcic sulphated alkaline water with a feebly acid reaction (acid due to dissolved carbon dioxide).
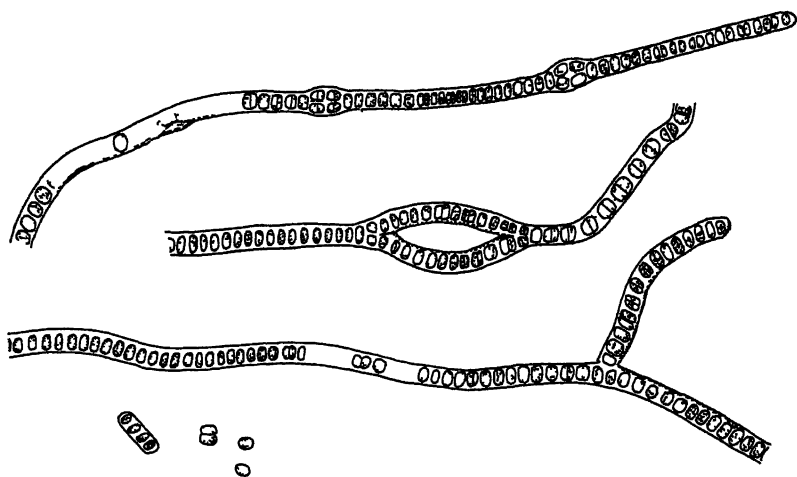
Fig. 29.—*Heterohormogonium schizodichotomum,* above, filaments with stages in branch development; below, free cells and young filaments (×1440).

Bacillosiphon, genus nov.

Plants tubular, tapering at both ends; consisting of a gelatinous tubular sheath and an axial core of numerous rod-shaped cells imbedded in a homogeneous matrix. Cells without regular arrangement, single or in pairs following division, mostly parallel with the length of the tubular plant; not forming filamentous cell rows or regular chains of cells Heterocysts, endospores, exospores, intercellular protoplasmic strands absent. Multiplication through the discharge of cylindrical, feebly motile planococci from the ends of the filiform plants.

Type species: *Bacillosiphon induratus.*

The systematic place of *Bacillosiphon* is questionable. The absence of exospores and endospores, and base-apical differentiation, eliminate it from the Chamaesiphonales. The irregular but definite arrangement of the cells, oriented in a direction parallel with the length of the plant,

suggests a relationship (but not a close one) to such genera as *Pseudon-cobyrsa* Geitler and *Lithocapsa* Ercegovic. The placing of the genus in the Entophysalidaceae is, nevertheless, tentative. The close similarity in general form to such Oscillatoriaceous genera as *Microcoleus* Desm. is apparently only a superficial resemblance, and in the absence of other more fundamental similarities seems to be of no importance.

A single species.
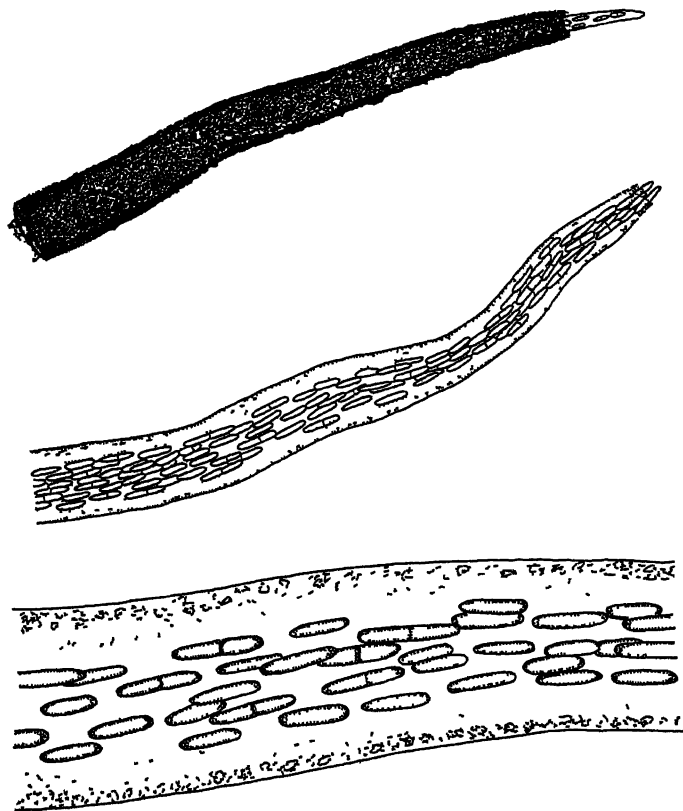
FIG. 30 —*Bacillosiphon induratus*, above, portion of plant with lime incrustation (×255), middle, apex of decalcified plant (×410); lower, detail of decalcified plant (×1020)

Bacillosiphon induratus, sp. nov.

Plants bright white, filiform up to 3 mm. in length, and tapering at both ends to blunt apices, up to 40μ in diameter in the middle portion and tapering gradually at the ends down to 6–10μ in diameter. Sheaths firm, hyaline and colorless, and heavily incrusted and indurated with lime, mostly opaque; lime

impregnation confined to the superficial portion of sheath, inner part of sheath and matrix of core in which cells are imbedded colorless and not indurated; matrix of core difficultly visible and soft   Cells cylindrical, with rounded ends. numerous and from few to 15 or 20 present in cross section; distinctly separated from each other by the gelatinous matrix, except following division; 1 8–2.2μ in diameter by 7–15μ in length. Cell contents homogeneous, blue-green. Cell division transverse. Multiplication through the liberation of single, sluggishly motile cells (planococci) from the open ends of the plants.

B. induratus is unique. Its white color, due to the heavy lime incrustation, is striking among Myxophyceae, and its general morphology is unparalleled among the unicellular and colonial blue-green algae.

While quite rare and local, *B. induratus* seems to be a regular component of the limital flora in certain springs at Mammoth. The type (OS. 33), from Minerva Terrace. and collections from Angel Terrace indicate its temperature range to be above 62° C. The type was at 70° C. and pH. 6.6.

CHAMAESIPHONALES Wettstein

Handbuch d. system. Botanik, 3rd ed., 1924

PLEUROCAPSACEAE Geitler

in Rabenhorst's Kryptogamen-flora, Bd. XIV, 1931.

Syn.: Pleurocapsales Geitler, Beih. Bot. Centralbl, 1925.

* Not known from the Yellowstone

II. Plants feebly filamentous or blastoparenchymatous and usually irregular two dimensional sheets, attached   XENOCOCCUS (p. 70)

MYXOSARCINA Printz

Subaer. Alg. South Afr., K Norske Vidensk. Selsk. Skrift., p 35. 1920.

Colonies unattached, spherical to irregularly spheroidal or ovoid, sometimes lobed, blastoparenchymatous with cells cuboidal, polygonal, or subspherical, flattened on adjacent faces and angular Cell divisions in three planes, cells often in irregularly cuboidal groups or packets. Sheath thin to moderately thick, distinct. Reproduction by endospores.
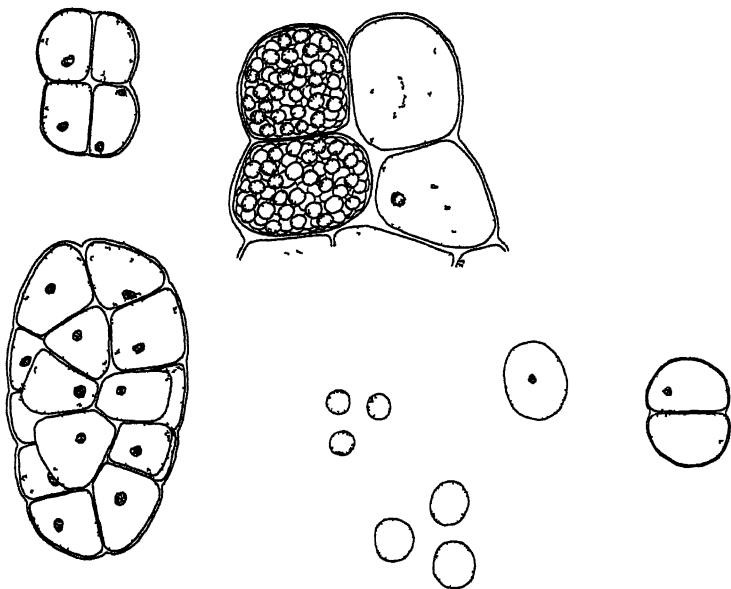
FIG. 31 —*Myxosarcina amethystina*, left, young and mature colonies (×2000), upper right, portion of colony showing endospore formation (×3000), lower right, germinating endospores and young sporelings (×2000)

Type species: *Myxosarcina concinna* Printz.

The species of *Myxosarcina* are known from tree trunks in South Africa, and from moors and swamps in Austria and Tyrol. None have been credited to either thermal sites or to America. In the Yellowstone the genus is rare.

A single Yellowstone species.

Myxosarcina amethystina, sp. nov.

Colonies occurring among other Myxophyceae, ovoid or less often subspherical or irregular, at maturity mostly 16 to 30-celled, 14–25μ by 28–40μ in size.

spherical to cuboidal when young. Cells close together but not tightly packed, flattened and angular by mutual pressure, but never sharply angular, 4.5–6.0μ in diameter, irregularly spheroidal to polygonal, with definite constrictions between cells. Cell contents blue-green, gray-violet, or steel blue, often with an amethyst tint; mostly with a single large granule, otherwise homogeneous. Matrix thin, hyaline, homogeneous, thinner between the cells than on periphery of the colony, about 0.3–0.5μ in thickness. Endospores spherical, cir. 0.5μ in diameter, produced in large numbers, often in all cells of the colony. Plant mass (when colonies are numerous enough to form visible masses) amythystine, friable.

In general aspect *M. amethystina* is close to *M. chroococcoides* Geitler. From this species it differs in its smaller cell size, more ovoid and less lobed colonies, and in its lack of the Sarcina-like packets of cells in the colonies. From the other species, *M. concinna* Printz, it differs by having less packed cells, fewer cells in the mature colonies, and in its general appearance. The large prominent granule in the cells of *M. amethystina* is not found in the cells of other species.

The plant has been found in a single site only, a spring at the source of Fairy Creek, above the entrance of the stream from Spray and Imperial Geysers, Twin Buttes Region. Here it grew in the floating algal mat that covered the warm spring pool. It was mixed with other Myxophyceae: *Oscillatoria princeps* var. *tenella* (of this paper), *O. terebriformis* (Ag.) Gom., *Phormidium tenue* (Mene.) Gom., *Anacystis thermalis* (of this paper), and incidental forms. The plant was frequent to abundant at temperatures from 37° C. to 46° C., and pH. 8.1. The type (no. 413) was at 42° C.

XENOCOCCUS Thuret

in Bornet & Thuret, Notes algologiques. 2, p. 73-75, Paris, 1880.

Colonies one to several layers of cells in thickness, either blastoparenchymatous, or at first blastoparenchymatous and later becoming filamentous, or crustaceous and obscurely blastoparenchymatous, attached and often "creeping," solitary or gregarious, with more or less evident polarity. Filaments often branched at maturity. Cells spherical, pyriform or irregularly polygonal, often in small packet-like groups. Matrix usually thin, hyaline, homogeneous, rarely lamellate. Endospores produced in large numbers, mostly in the terminal cells.

Type species: *Xenococcus Schousboei* Thuret.

The species of *Xenococcus* grow mostly on filamentous algae, either in fresh or salt water, thermal species have not been reported.

A single Yellowstone species.

Xenococcus yellowstonensis, sp. nov.

Cells spherical to subspherical, often angular by mutual pressure 6–10μ in diameter by 7–11μ in length, bright blue-green, united into an irregular botryoidal or foliose or almost filamentous prostrate thallus of microscopic size, at most less than 150μ in greatest dimension; thallus 1–3 cells in thickness, 1–5 cells broad, and up to 18 cells in length. Sheaths hyaline, homogeneous, up to 1.8μ in thickness. Most or all cells of mature thalli producing numerous endospores 0.6–1.0μ in diameter.
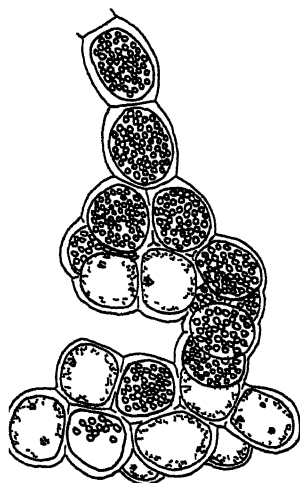
FIG. 32.—*Xenococcus yellowstonensis* (×1000).

X. yellowstonensis is close to *X. Schousboei* Thuret, from which it differs in having thicker, less extended strata, less crowded and more rounded cells, and a homogeneous, not lamellate tegument. It can be readily separated by these characters; it is totally foreign to the marine, non-thermal *X. Schousboei* in habitat.

The species occurs on and in the strata of other Myxophyceae, especially those of *Chroococcus* and *Phormidium*. The known range of *X. yellowstonensis* is very limited. It was found only in one of the Meadow Springs cir. one-quarter mile north of Semicentennial Geyser. There it was growing in water ranging from 51° to 65° C. and at about pH. 5.4. The type (no. 193) was at 62.2° C. and pH. 5.4. At best the plant is rather rare in this spring, although adequate material was easily procured.

DERMOCARPACEAE Geitlér

Synopt. Darst. Cyan., Beih. Bot. Centralbl. pt. 2: p. 247, 1925.

KEY TO THE YELLOWSTONE GENERA.

I. Plants spherical, unattached, without base-apical differentiation.

PLUTO (p. 72)

II. Plants attached, with base-apical differentiation.   DERMOCARPA (p. 74)

Pluto, gen. nov.

Plants unicellular, spherical, without base-apical differentiation, with a thin gelatinous tegument; vegetative division absent: multiplication through endospores cut out with the division planes at angles of 120° to each other, endospores 4 in each cell.

Type species: *Pluto caldarius* (Tilden).

The closest relatives of this genus are *Dermocarpa* Crouan and possibly *Myxosarcina* Printz. In *Myxosarcina* the repeated cell divisions are at right angles to each other, and the endospore formation is of the usual type. Unlike *Dermocarpa, Pluto* is unattached, perfectly spherical, and produces only four endospores in each cell. The tripartite group of spores in *Pluto* is unique among the Myxophyceae. The genus is based on the single species *Pleurocapsa caldaria* (Tilden) Setchell. *Pluto* is totally unlike *Pleurocapsa* in lacking vegetative divisions, never forming filaments, and in producing fewer endospores, which are formed in each normal cell.

The species, described from the Yellowstone, is found in acid, hot waters. Its occurrence on Roaring Mountain, in the Mud Volcano, and in other places where the forces of vulcanism are so much in evidence has caused me to dedicate this genus to the God of the Underworld, Pluto.

A single species.

Pluto caldarius (Tilden), comb. nov.

Syn.: *Protococcus botryoides* f. *caldaria* Tilden, 1898.
     Chroococcus varius A. Braun (by Tilden, 1896).
     Pleurocapsa caldaria (Tilden) Setchell, 1901, in Collins, Holden and
       Setchell: Fas. 18, no. 851.

Plant mass flocculent, yellowish to livid blue-green or arsenic green. Plants unicellular, spherical or rarely angular by mutual pressure, 4–6μ in diameter; cell contents homogeneous, pale green. Tegument thin, homogeneous, and hyaline, often granular in spots with a precipitate of silica. Endospores 4, in a tripartite group when first formed, angular, becoming spherical before libera-

tion, 1.5–2.5μ in diameter, liberated through the disintegration of the parent cell membrane.

In the acid waters of the Yellowstone this species is very common. Tilden (1898) reported it from several localities: Norris Geyser Basin: Constant Geyser, 49° C., Frying Pan Group; unnamed spring, 38° C.; and Green Spring (not the Green Spring of the Upper Geyser Basin, possibly Semicentennial Geyser before the eruption of 1922), north of Norris Geyser Basin. Elsewhere it has been reported only from the Devil's Kitchen "Geysers", Sonoma, California, where it was found by Setchell and Hunt (Setchell, 1901).
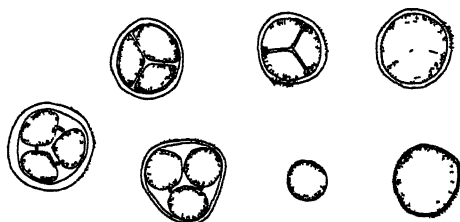
Fig. 33.—*Pluto caldarius* (Tilden), stages in development and sporulation (×1500).

I have found the species in numerous springs including: Mud Volcano, Dragon's Mouth Spring, and associated springs; Great Sulphur Spring and smaller springs in the Crater Hills; Roaring Mountain, Lemonade Creek, Semicentennial Geyser, Frying Pan, and Obsidian Creek; Blue Geyser, Apple Green Geyser, Iris Spring, and others in the Norris Geyser Basin; springs in the Monument Geyser group; and in several isolated springs. The abundant growth of this alga is the most striking feature of many springs, especially in the Norris Basin. Several, notably Apple Green Geyser, Emerald Spring, and the Green Dragon Springs, have been named in allusion to the livid and beautiful strata of *Pluto* occurring in their waters. The pH. range for the species as I have found it is from 2.6 to 5.4; the temperature range 34° C. to 80.2° C. For a single species to live and develop normally through the temperature range that *P. caldarius* inhabits is highly unusual. The species is one of the six species of Myxophyceae I have found in the Yellowstone at temperatures of 80° C. or above. The site at which it was found growing at the highest temperature (80.2° C.) was at the edge of the Great Sulphur Spring in the Crater Hills. This spring is actively boiling and semi-eruptive; the water in the crater is around 91° C. Every fifteen to thirty minutes water at about 90° C. flowed over

the growth of *P. caldarius* and at such times its temperature was almost at the boiling point. Between these intermittent scalding baths a slow trickle of water kept the alga wet. The lowest temperature reached at the edge of the algal growth, during the period of observation (five consecutive days) was 80.2° C. Undoubtedly *Pluto caldarius* can endure water with a temperature as high as 90° C. without injury.

P. caldarius was found to be the most satisfactory index species of the sharply acid waters of the Park. When the growth was abundant, the acidity was regularly below pH. 5.0.
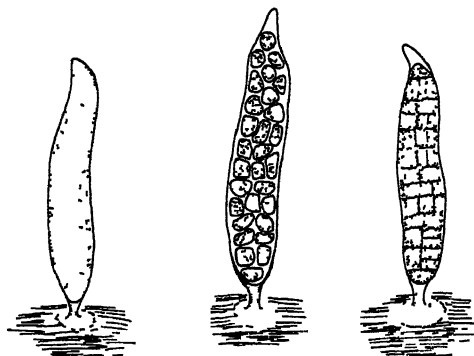
FIG. 34.—*Dermocarpa rostrata,* mature and sporu-
lating plants (×1750).

DERMOCARPA Crouan

Ann. Sc. Nat. Bot., Ser. 4, 9, p. 70, 1858.

Plants unicellular or with one-celled sporangium and a smaller stalk cell, attached, with base-apical differentiation, gregarious or solitary. Cells spherical, ovoid, pyriform, or vase-shaped, with a gelatinous stalk or attaching disk, less often with a special stalk cell at base of plant. Endospores 4 to many, formed by simultaneous or successive divisions and using all or most of the protoplasm of the cell, sometimes beginning at the apex and progressing downward. Endospores liberated through an apical slit, by dehiscence of the apical portion of the cell wall, or by gelatinization of the entire cell wall.

Type species: *Dermocarpa violacea* Crouan.

The majority of the many species are marine, several are of fresh water; no thermal ones have been noted; they occur chiefly on various algae, less often on mosses and other water plants.

A single Yellowstone species.

Dermocarpa rostrata, sp. nov.

Plants solitary or gregarious, attached to larger algae. Cells elongate, sub-cylindrical, irregular, tapering toward both base and apex; 4–6μ in diameter

by 15–25μ in length, pale blue-gray, with minutely granular or almost homogeneous contents. Apex asymmetrically blunt-pointed and bent. Base of cell evenly rounded, without stalk cell, with a gelatinous stalk 2–4μ in length and 1–2μ in diameter rising from a disk-shaped, hyaline or brownish, thin "foot" 4–7μ in diameter. Endospores numerous, 15–40, angular at first, becoming spherical, 1.5–2.5μ in diameter, escaping through an apical slit in the membrane. Divisions to form endospores simultaneous or almost so, no protoplasm left in sporulating cells.

This species is as distinct as any of the many representatives of *Dermocarpa*. It shows possibly closer resemblance to the marine *D. cuspidata* (Reinsch) Geitler than to any other. It is considerably larger than this species, possesses a definite stalk, has an asymmetric although pointed apex, and a thinner membrane. In *D. cuspidata* endospore formation has not been observed.

D. rostrata was found growing abundantly, along with *Chamaesiphon incrustans* Grunow, on dead and dying *Cladophora*, (type: no. 432) in the Firehole River opposite the Biscuit Basin at 22.5° C. and pH. 8.2. The species gives no evidence of being thermal but it has not been found in waters of a normal temperature for the region (cir. 8–12° C. in the Firehole River where not heated by thermal waters, in the summer).

CHAMAESIPHONACEAE Geitler

Synop. Darst. Cyan., Beih. Bot. Centralbl., pt. 2: p. 249, 1925.
Not Chamaesiphonaceae Borzi in N. Giorn. Bot. Ital., 1882.

A single genus.

CHAMAESIPHON A. Braun et Grunow

in Rabenhorst, Fl. Eur. Alg. 2, p. 148, 1865.

Plants unicellular, ellipsoidal, cylindrical, claviform or pyriform, spherical when young, with base-apical differentiation, attached and usually epiphytic, mostly erect or suberect, solitary, gregarious, or aggregated into masses; basal part of cell forming an attaching structure, sessile or stipitate; distal end rounded and producing by abstriction a series of one to many spherical exospores, that are shed immediately after formation or later. Pseudovagina (sheath) often lamellate, hyaline, golden, brownish, blackish, or reddish, open above in mature plants. Cell contents homogeneous or finely granular, often with a single prominent granule, blue-green, olive-green, grayish, violet, or reddish violet.

Type species: *Chamaesiphon confervicola* A. Braun.

The several species of *Chamaesiphon* inhabit flowing or standing fresh water, wet or periodically moist rocks, and are attached to the substratum

directly or more frequently to larger algae, mosses, and other aquatic plants. *C. incrustans* Grunow, a common, chiefly non-thermal species, has been reported from warm springs at Los Baños, Porto Rico, where it occurred on *Oedogonium*. It is safe to assume that it was growing at not above 35° C., since *Oedogonium* rarely occurs at temperatures as high as 30° C. The Yellowstone observations tend to strengthen the status of *Chamaesiphon* as a non-thermal group of species.

KEY TO THE YELLOWSTONE SPECIES

I. Cells up to 3μ in diameter by up to 6μ in length.
   1. Pseudovagina thin, almost invisible, cells up to 2.5μ in diameter.
                                                                 C. minutus 1.
   2. Pseudovagina thick, easily visible, cells up to 1.8μ in diameter.
                                                                 C. minimus 2.
II. Cells 4–8.5μ in diameter by 7–30μ in length.   *C. incrustans* 3.

1. CHAMAESIPHON MINUTUS (Rostaf.) Lemm.

Krypt.-Fl. Mark Brandenb., 3, p. 98, 1910.

Cells solitary or gregarious, almost cylindrical or obscurely egg-shaped, sometimes lightly curved, up to 3μ in diameter and up to 6μ in length (usually not over 5μ), pale blue-green or olive-green, attached by a broad short gelatinous stalk. Pseudovagina thin and delicate, colorless. Exospores mostly single, spherical, 2.0–2.5μ in diameter. Cell contents mostly with a prominent, usually basal granule.
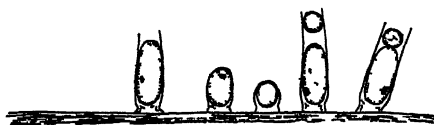
FIG 35 —*Chamaesiphon minutus* (Rostaf.) Lemm. (×1400).

C. minutus is poorly known in the Western Hemisphere. It has not been credited to thermal sources.

In the Yellowstone it occurs in the Firehole, Gibbon, and Madison rivers in non-thermal waters. In the Firehole it extends into portions of the river that are distinctly warmed by the overflows of hot springs. Opposite the Biscuit Basin it was found in water up to 26° C., growing on *Cladophora*, along with *Dermocarpa rostrata* (of this paper) and other epiphytic algae (nos. 431, 432). The species is evidently non-thermal and extends its range into at most tepid waters. The water at this site had an alkalinity of pH. 8.2; in the strictly non-thermal sites the water ranged from pH. 6.8 to 7.4.

2. CHAMAESIPHON MINIMUS Schmidle

Beitr. Fl. Afrika, Engler's Bot. Jahrb. 30, p. 62, 1902.

Cells solitary or gregarious, cylindrical with rounded ends, straight, 1.8μ in diameter by up to 3.5μ in length, blue-green, attached by a broad short gelatinous stalk. Pseudovagina thick, easily visible, colorless, conspicuous even around the cell body. Exospores single, spherical, cir. 1.5μ in diameter. Cell contents homogeneous, without prominent granules.

Known only from equatorial Africa and eastern Europe, the species is quite an interesting addition to the American flora.

In the Yellowstone it has been found in a single site only, but over a period of four years time. It grew on *Oedogonium* and *Cladophora* in the Firehole River opposite the Biscuit Basin at cir. 20–24° C. and at pH. 8.2 (no. 432). At this point the waters from several hot springs enter the river and keep the water a little warmer than that in the river above the springs. The plant is evidently non-thermal and is to be found only in cool locations, but it has not been observed in strictly meteoric waters.
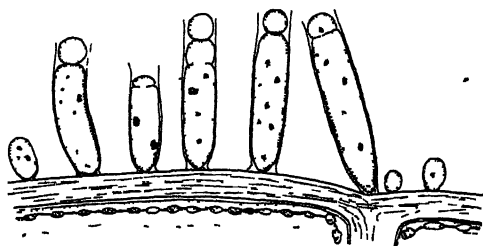
FIG. 36 —*Chamaesiphon incrustans* Grunow
(×720).

3. CHAMAESIPHON INCRUSTANS Grunow

in Rabenhorst, Fl. Eur. Algar. 2, p. 149, 1865.

Plants solitary or gregarious, often densely so; cells vase-shaped to almost cylindrical, straight or slightly curved, up to 8.5μ in diameter and tapering to 1–3μ at the base, up to 30μ in length, blue-green, olive-green or, less often (in deep water), reddish violet. Pseudovagina thin, firm, hyaline. Exospores 1–3, rarely more, cir. 6–7μ in diameter. Cell contents finely granular. Attached at base by a slender, very short gelatinous stalk.

Growing in standing or running fresh water on algae, mosses, and other water plants, *C. incrustans* is the best-known species of the genus. It is found generally in the United States. The only record of the

plant from thermal sources is that of Sintenis (Möbius, 1888) from a warm spring in Porto Rico.

In the Yellowstone it is frequent in the streams and ponds. It has been noted chiefly on *Oedogonium* and *Cladophora*. In the Firehole River opposite the Biscuit Basin it was found at 22.5° C. (nos. 431, 432), at pH. 8.2. It is typically non-thermal.

Oscillatoriales, nomen novum

Syn.: Hormogoniales Wettstein, Handbuch der systemat. Botanik, 3rd. Ed., 1924.

Hormogoneae, of many authors.

Filamentous Myxophyceae, with the cells of the trichome joined by often minute and difficultly visible, intercellular, protoplasmic strands (plasmodesma).

KEY TO THE FAMILIES

I. Trichomes branching, the branch initial cell arising by a division parallel to the polar axis of the cell.
  1. All branches strictly lateral.
    A. Branches all of a single type (often different from the main filament), never ending in heterocysts.   STIGONEMATACEAE (p. 82)
    B. Branches of two sorts, one type long and often tapering, the other short and often ending in a heterocyst.   NOSTOCHOPSACEAE (*)
  2. Part of the branches (especially the upper) dichotomous or subdichotomous.
    A. Filaments free, or at most in a gelatinous matrix.
      a. Branching subdichotomous and lateral; plant mass gelatinous.   CAPSOSIRACEAE (*)
      b. Branching dichotomous and lateral; plant mass fibrous, not gelatinous.   LORIELLACEAE (p. 79)
    B. Thallus nematoparenchymatous, with laterally united more or less radially arranged filaments.   PULVINULARIACEAE (*)
II. Trichomes unbranched (filaments often branched); all cell divisions at right angles to the polar axes of the cell (except (?) rarely in the formation of endospores); trichomes always monosiphonous.
  1. Trichomes with "V" branching (sometimes suppressed).   MASTIGOCLADACEAE (p. 88)
  2. Trichomes without "V" branching, often with ordinary false branching.
    A. Filaments with sharp cup-like basal attaching stalk; heterocysts absent; filaments tapering at tips; epiphytic on water mites.   SOKOLOVIACEAE (*)
    B. Filaments otherwise, without cup-like basal attaching cell (often basally attached, often tapering, heterocysts present or absent).
      a. Trichomes with false branching.

* Not known from the Yellowstone.

    *. Trichomes not tapering; never ending in colorless hairs.
                                  SCYTONEMATACEAE (p. 92)
   **. Trichomes tapering toward the apices, mostly ending in color-
      less hairs.
         !. Plants consisting of two-ended, more or less prostrate fila-
           ments with more or less erect, tapering branches or filament
           apices.   HAMMATOIDEACEAE (p. 101)
        !!. Plants consisting of tapering, base-apically specialized fila-
           ments, tapering at a single end only.
                              RIVULARIACEAE (p. 106)
 b. Trichomes without false branching (often with false-branching
    filaments).
      *. Heterocysts present.
        !. Sheaths firm, thin, not slimy, not confluent.
                        MICROCHAETACEAE (p. 127)
        !!. Sheaths soft and gelatinous or slimy, often absent, often
          confluent.   NOSTOCACEAE (p. 130)
 **. Heterocysts absent.   OSCILLATORIACEAE (p. 139)

LORIELLACEAE Geitler

Synopt. Darst. Cyan., Beih. Bot. Centralbl., pt. 2, p. 41, 1925.

Syn.: Lorielleae Borzi pro parte, Studi s. Mixof., in N. Giorn. Bot. Ital., p. 21, 1914.

A single Yellowstone genus.

Colteronema, gen. nov.

Stratum fibrous, made up of free, more or less horizonal, mostly laterally branched filaments and more or less erect, mostly dichotomously branched ones. Filaments cylindrical, monosiphonous, with firm, thick sheaths. Growth apical. Heterocysts absent. Resting cells unknown. Hormogonia produced at ends of branches.

Type species: *Colteronema funebre.*

The dichotomous branching of *Colteronema,* produced by the longitudinal division of an apical cell sets the genus apart from the majority of the true branching Myxophyceae. Lateral branching occurs in *Colteronema* quite frequently in addition to the dichotomy; the lateral type is found mostly in the prostrate filaments and in the older portions of the filaments. In the more erect filaments repeated dichotomy is regular. Of the genera of blue-greens that possess either dichotomy or subdichotomy, *Hyphomorpha* Borzi, *Loriella* Borzi, *Stauratonema* Frémy, and *Capsosira* Kütz, have heterocysts; *Pulvinularia* Borzi, a nematoparen-

chymatous thallus; *Letestuinema* Frémy, a gelatinous hemispherical thallus; and *Desmosiphon* Borzi, several aberrant features, including the loose structure of the filaments and a tendency to break up into a chroococcoid status. By these features *Colteronema* may be distinguished in each case. Its closest relative seems to be *Hyphomorpha.* I have placed the genus in the family Loriellaceae Geitler with *Hyphomorpha* and *Loriella.*

The genus *Colteronema* has been named in honor of John Colter, the first white man to enter the Yellowstone.

A single species.

1. Colteronema funebre, sp. nov.

Stratum extended, membranous to leathery, fibrous, up to 1 mm. in thickness, blue-black to dull greenish brown, terrestrial. Filaments usually crooked, somewhat roughened, cylindrical, slightly or not at all torulose, densely packed, abundantly branched, up to 1 mm. or more in length and 5–8μ in diameter. Sheath firm, thick, rarely hyaline, usually golden to yellow-brown, with divergent lamellae, at tips usually transversely striated. Trichomes moniliform or nearly so, 3–5.3μ in diameter, strongly constricted at the cross walls. Cells subcylindrical with rounded ends to ovoid, 1–3 diameters in length, 4–12μ long. Cell contents often with prominent polar granules, blue-green. Trichome tips ordinarily unmodified, with less prominent constrictions between the apical and subapical cells only; at points of dichotomy swollen and with a bulbous apical cell up to 9μ in diameter. Dichotomous branching originating by the longitudinal division of a swollen apical cell: lateral branching originating by a longitudinal division of an intercalary cell. Hormogonia few-celled, infrequent.

The skin-like dark greenish brown to blue-black stratum of the species covered the damp rock and soil for several feet above and around a small boiling spring in the Meadow Springs Group. The steam from the springs is so abundant that the algae are kept uniformly moist but not wet. Collecting the species was a very severe problem, since it involved, with the greatest of care, an excellent steam bath at about 85° C. The algal stratum was much cooler—ranging from 36–43° C., where the growth was more abundant. The type (no. 177) was at 38° C. It is notable that there may be a great range of temperature in a distance of a few centimeters. In this case a temperature determination made with the bulb of the thermometer partly exposed to the steam that might easily blow around it could be highly erroneous. The alga has not been found elsewhere, although similar sites have been searched systematically. The growth in this single site has been intact and abundant for at least four years consecutively.
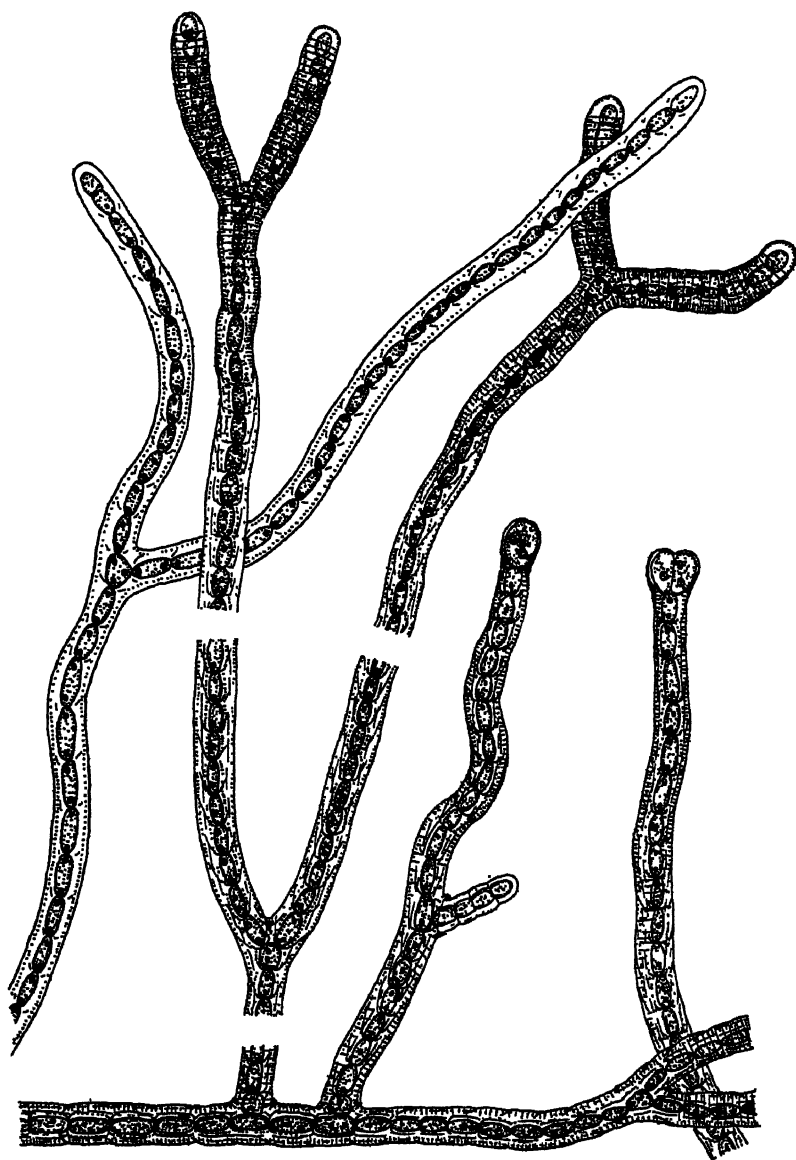
Fig. 37.—*Colteronema funebre,* portions of filaments with dichotomous and lateral branching (×840).

STIGONEMATACEAE Geitler

Synopt. Darst. Cyan., Beih. Bot. Centralbl. 41, pt. 2, 1925.

Syn.: Eustigonemeae Borzi, Studi s. Mixoph., in N. Giorn. Bot. Ital., p. 21, 1914.

KEY TO THE YELLOWSTONE GENERA.

I. Heterocysts present.
    1. Filaments free; not agglutinated into bundles or corded strands.
        A. Filaments prostrate, dorsi-ventral, bearing branches on the upper side only; branches thinner than the main filaments and with longer cells.
                FISCHERELLA (p. 82)
        B. Filaments not usually dorsi-ventrally modified; branches arising on all sides or unilateral, branches little if any thinner than the main filament and with cells little or not at all longer.
           a. Old trichomes at least in places polysiphonous; heterocysts in part lateral.   STIGONEMA (p. 83)
           b. Old trichomes monosiphonous, rarely for short distances with two rows of cells; heterocysts intercalary.   HAPALOSIPHON (p. 84)
    2. Filaments more or less parallel, in bundles or corded strands.
                THALPOPHILA (p. 87)
II. Heterocysts absent.   ALBRIGHTIA (p. 85)

FISCHERELLA Gomont

Journ. de Bot. 9, p. 52, 1895.

Thallus consisting of dorsi-ventrally specialized, prostrate and creeping, usually contorted main filaments bearing on their dorsal sides erect, straight to flexuous, slender branches. Main filaments monosiphonous or more often polysiphonous, usually crooked, with large spherical or subspherical cells; branches monosiphonous, more slender than the main filaments, with smaller, usually elongate, cylindrical cells. Sheaths at first narrow, later broad, often lamellate, specially in the main filaments. Cells in the old filaments often chroococcoid, and with concentrically lamellate sheaths. Heterocysts intercalary or lateral. Hormogonia formed at the ends of the side branches. Resting cells present in some species.

Fischerella is separated from *Hapalosiphon* Naeg., *Stigonema* Ag. and *Westiella* Borzi by at best rather unsatisfactory characters. The genus intergrades with *Stigonema* in particular.

The species of *Fischerella* occur on damp soil, rocks, and tree trunks; in fresh water; and one species in warm springs. The thermal species, *F. thermalis* (Schwabe) Gom., is the only one that has appeared in the Yellowstone collections. It and its variety *mucosa* Lemm. are known from hot waters in Hawaii; *F. thermalis* has been found in hot springs in Europe, and in non-thermal waters in both Europe and North America.

A single Yellowstone species.

1. FISCHERELLA THERMALIS (Schwabe) Gomont

Journ. de Bot. 9, p. 52, 1895.

Stratum woolly, cushion-like, up to 1 mm. in thickness, often extended, blue-green, olive-green, or blackish. Main filaments prostrate and creeping, crooked and twisted, thickly packed, mostly with two rows of cells, less often with one or three rows, 10–13µ (less often up to 18µ) in diameter; sheaths moderately thick, lamellate, golden brown. Side branches erect, cylindrical, single or in groups, 6–9µ in diameter; sheaths close, hyaline to pale yellowish, feebly or not at all lamellate. Cells 4.2–8µ in diameter, short, cir. 1 diameter in length, blue-green. Heterocysts intercalary and lateral. Hormogonia 3–6-celled.

In the United States *F. thermalis* has been reported from New Hampshire by Farlow (1883). It apparently is not common in North America. It has been found chiefly on damp to wet rocks and in warm water.

While rare in the Yellowstone, it is locally common in the Lower Geyser Basin around the Firehole Lake. There it grew on the damp earth and at the edges of small pools at temperatures of from 22° C. to 36.7° C. (no. 402).

STIGONEMA Agardh

Syst. Alg., p. 22, 1824.

Stratum consisting of free, irregularly laterally branched, mostly irregular filaments. Old filaments monosiphonous or more often polysiphonous, with apical growth and often with a definite apical cell and segmentation of the cells cut off from it. Side branches becoming like the main filament as they age. Sheaths in young filaments narrow; in older ones usually broad, often lamellate, and often colored; old cells often with concentrically lamellate sheaths. Heterocysts intercalary and lateral, usually in both positions in a single plant. Hormogonia 2–many-celled, usually few-celled, formed at apices of young branches. Chroococcoid stage present.

The species of *Stigonema* are confined to damp situations and to fresh water. The majority are terrestrial and live on damp soil, rocks, tree trunks, etc.; the fresh water species are chiefly benthonic; one is planktonic; a single species occurs in the lichen *Epheba*. Thermal species have not been reported.

In the Yellowstone thermal springs the genus is insignificant.

A single Yellowstone species.

1. STIGONEMA HORMOIDES (Kütz.) Bornet & Flahault

Revision Nost. het., p. 68, 1887.

Syn. *Sommierella hormoides* Borzi, N. Giorn. Bot. Ital. 24, p. 116, 1917.

Filaments prostrate, densely woven, moderately long, forming a thin fibrous brownish-black stratum. Main filaments 9–15µ in diameter; irregularly and

sparingly branched. Side branches erect, almost as thick as the main filaments, 7–12µ in diameter, crooked. Sheaths thick, colorless, yellow, or yellow-brown. Trichomes mostly monosiphonous, occasionally with two rows of cells for a short distance. Heterocysts lateral and intercalary. Chroococcoid stage present.

As an abundant, cosmopolitan species, *S. hormoides* is to be expected in any locality presenting a favorable environment. The plant is well known in North America, but had not previously been reported from the Yellowstone. It inhabits, usually, moist rocks, peaty damp soil, shallow pools, and often occurs in the slime of gelatinous Myxophyceae.

In the Yellowstone it is found in non-thermal sites quite frequently; and it encroaches on thermal habitats in many places. The highest temperature at which it was found is 32.2° C. (no. 402); at this point, the damp bank of the Firehole Lake, Lower Geyser Basin, it was abundant, occurring with *Scytonema caldarium terrestre* (of this paper). The alga is clearly a non-thermal species.

HAPALOSIPHON Naegeli

in Kützing. Spec. Alg., p. 894, 1849.

Stratum consisting of free, twisted, irregularly laterally, often unilaterally branched filaments. Filaments regularly monosiphonous, except for single cells that have divided lengthwise (in preparation for branching). Branches like the main filaments, but often slightly thinner and with longer cells. Growth mostly apical, often intercalary; without a well-developed apical cell. Sheaths firm, mostly narrow, either homogeneous or lamellate, hyaline or colored. Heterocysts intercalary. Hormogonia usually formed on the side branches. Resting cells often present.

The limits of *Hapalosiphon* are somewhat arbitrary. The regularly intercalary heterocysts, uniseriate trichomes, the resting cells (when present) separate the species roughly from those of *Stigonema, Fischerella,* and *Sommierella* Borzi.

The habitats of the several species include standing and slowly flowing fresh water, acid and boggy waters. A single species, *H. fontinalis,* occurs in thermal springs.

A single Yellowstone species.

1. HAPALOSIPHON FONTINALIS (Ag.) Born.

Bull. Soc. Bot. France 36, p. 156, 1889.

Plants occurring in floccose tufts; blue-green to brown in color, 1–3 mm. high. Main filaments tangled, creeping, usually twisted and crooked, abundantly branched, 12–24µ in diameter, mostly monosiphonous, but here and there

with 2 or 3 rows of cells for short distances. Branches erect, thinner, 9–12μ in diameter, monosiphonous. Cells roughly isodiametric, spherical to quadrate in the main filaments, cylindrical in the branches, and 1–2 diameters in length. Sheaths more or less thick, colorless when young, becoming golden brown, homogeneous or somewhat lamellate in the old filaments, often slightly constricted opposite cross walls of old filaments. Heterocysts intercalary, quadrate to cylindrical. Hormogonia cir. 6μ in diameter by 100–300μ in length, with 14–50 cells.

This variable, cosmopolitan species is well known in North America. It has been reported from Alaska (Saunders) to the West Indies (Jamaica by Humphrey), from Maine (Harvey) to Minnesota (Tilden), but has not been noted in thermal sites in this country. It has been reported from hot springs in Europe and Africa. In the Yellowstone it is not frequent. It has been observed twice in the present investigation—once in a non-thermal pond on leaves of *Nymphaea advena* (Lily Pad Pond, cir. 16° C.) and once in a tepid pool in the Upper Geyser Basin (26° C., pH. 6.8). The plant is unimportant and is not, at least in the Yellowstone, a thermal alga.

Albrightia, gen. nov.

Plant mass made up of free, laterally branching filaments. Filaments more or less uniformly cylindrical, with a single row of cells, and with apical growth. Branches with the same diameter and form as the main filaments. Sheaths ample, firm, homogeneous or lamellate. Heterocysts and resting cells absent. Hormogonia few-celled. Chroococcoid stage present.

Type species: *Albrightia tortuosa.*

Albrightia is a typical member of the Stigonemataceae. The general aspect of the genus is quite similar to that of *Hapalosiphon* Naeg. and *Stigonema* Agardh. In its lack of heterocysts it resembles *Rosaria* Carter. From *Rosaria* it differs quite markedly—the even, moderately thick sheath, the cylindrical filaments, the normal cell wall, the typical apical growth are characteristic of *Albrightia,* and ally it with the better-known Stigonemataceous genera. The presence of a well-marked chroococcoid stage recalls *Stigonema,* while the monosiphonous filaments suggest *Hapalosiphon.*

This genus has been named in honor of Horace M. Albright, until recently National Park Service Director, the one who in recent years has done possibly more than any other single man to preserve the Yellowstone in its natural state, and to whom all who visit the Park for study or pleasure owe sincere gratitude.

A single Yellowstone species.

1. **Albrightia tortuosa,** sp. nov.

Stratum poorly developed, occurring mostly as blue-green flecks on the surface of other Myxophyceae, or intermingled more or less intimately with them; dull blue-green, gelatinous-fibrous. Filaments mostly irregularly twisted, coiled, or less often flexuous, up to 1 mm. in length, branching sparsely with the branches at wide angles, without differentiation between branches and main filaments; 5.0–8.5μ in diameter (rarely thicker in old filaments). Trichomes monosiphonous except at points of branching, moniliform, distinctly constricted at the cross walls; 3.2–4μ in diameter. Sheaths firm, homogeneous or in very old filaments feebly lamellate, hyaline or in very old filaments yellowish, around 2μ thick (rarely up to 3.5μ in old filaments). Cells blue-green, cask-shaped and
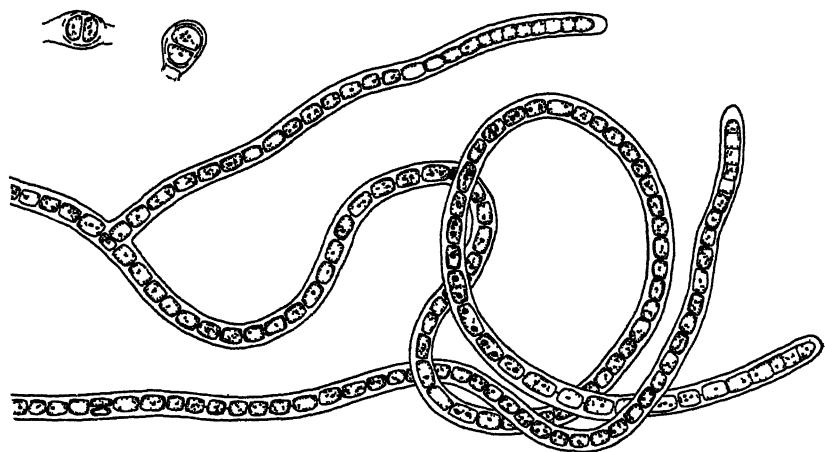
Fig. 38 — *Albrightia tortuosa,* typical filaments; upper left, chroococcoid pairs of cells from old filaments (×670)

swollen except at the apices, with granular contents and often with one to a few prominent granules, often distinctly separated in life, 1.0–2.2 diameters in length, 3.3–9.0μ long. Apices rounded, with trichomes cylindrical or almost so, and with the cells shorter. Chroococcoid groups of cells in old filaments, often persisting after the disintegration of the filaments. Hormogonia infrequent, mostly 2–few-celled.

The plasmodesma are unusually prominent and in healthy living filaments are often visible when the cells are separated a short distance.

The plant is usually present among and on *Scytonema caldarium terrestre* (of this paper), and *Schizothrix thermophila* (of this paper) on the moist warm flats and pool edges of the Firehole Lake section of the Lower Geyser Basin. It is regularly found emersed, and it is not found even in temporary eruption pools. Its thermal range, as far as it has

been found, is 29–43° C., its pH. range 8.0–8.9. The type (no. 401) is from the bank of Firehole Lake, growing at 34° C. The species has not been collected outside of the Lower Geyser Basin.

THALPOPHILA Borzi

Atti Congr. Milano, 1906.

Plant mass composed of fascicles or corded strands made up of mostly parallel, numerous filaments; the filaments branching sparingly with the branches soon lying parallel to the parent filament; filaments containing a single trichome each. Filaments all essentially alike, but the older ones often becoming contorted and crumpled; branches of the same diameter and nature as the main filaments. Sheaths thick, lamellate, gelatinous, and slimy without. Heterocysts intercalary; hormogonia absent (or unknown); resting cells in rows, with smooth walls.

Type species: *Thalpophila cossyrensis* Borzi.

Up to the present only a single species, *T. cossyrensis*, has been credited to the genus. This species has so far been found growing only on igneous rock in the vapor from a hot spring on Pantelleria (a small island in the Mediterranean Sea south-west of Sicily).

A single Yellowstone species.

1. Thalpophila imperialis, sp. nov.

Thallus, in the form of long, occasionally branched, occasionally anastomosed, soft, flexible, gelatinous, corded strands. attached by the basal ends or broadly along the sides; rarely many strands grow together and coalesce to form an almost solid stratum; brilliant blue-green except when (often) incrusted with epiphytes; cords up to 1.5 cm. in diameter and up to 2 dm. in length. Filaments numerous (up to thousands, in a single strand) usually more or less regularly parallel, 4–6μ in diameter, occasionally branched, the branches identical with the main filaments, single, in pairs or rows, most numerous in the basal part of the plants. Trichomes cylindrical when young, beaded or moniliform in older portions, 3–4μ in diameter; cells slightly longer than their diameter, 1.2–2.5 diameters in length, longer near the tips of the trichomes; terminal cells conical and pointed; cell contents clear blue-green, with one to a few refractile granules mostly near center of cells. Sheaths thin, distinct, and homogeneous in younger parts; thick, faintly lamellate, and confluent in older parts; always colorless and usually almost transparent; soft and gelatinous, slimy without. Heterocysts intercalary, not numerous, elongate, and swollen, 4.0–4.5μ in diameter by 6–13μ in length, 1.5–3.0 diameters long, frequently functioning as endosporangia and producing two endospores. Resting cells in rows in older parts of plants, often very numerous, up to 12–70 in a row, usually on both sides of a heterocyst, short-cylindrical, swollen, 4–5μ in diameter by 5–7μ in length, the walls slightly thickened, smooth, contents granular, dark blue-green.

In one collection the majority of the heterocysts contained endospores. The occurrence of spores in the heterocysts has not been commonly observed in the Myxophyceae and it is noteworthy that those species in which they have been observed are chiefly in the Family Nostocaceae (*Nostoc, Anabaena*).

T. imperialis differs from *T. cossyrensis* Borzi in many details: it is aquatic; the plant mass is much larger; the trichomes, filaments, and sheaths are thinner; the resting cells are smaller and the heterocysts different in shape. These two species, quite similar in microscopic aspect as well as in general morphology, present an interesting problem in phyto-geography. Their restriction to the Yellowstone and to Pantelleria, and to thermal habitats is difficult to interpret.
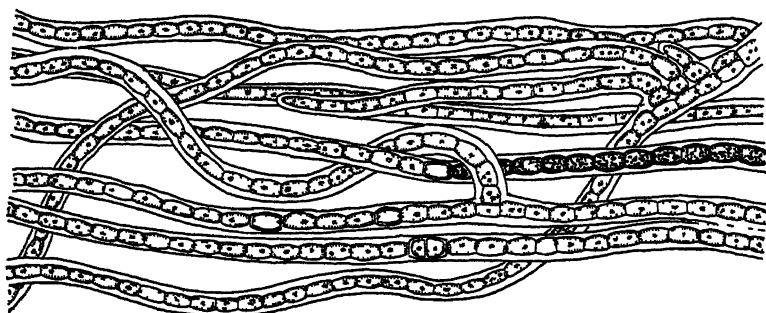
Fig. 39.—*Thalpophila imperialis,* filaments with characteristic branching; row of resting cells in one filament and spores in heterocysts in a second (×700).

The present data indicate that *T. imperialis* is very local in distribution, confined to the rill from Spray Geyser and to Imperial Creek (overflow from Imperial Geyser Crater) below the junction with Spray Geyser rill. The alga is restricted to the rapid current in quite warm water at 48–60.4° C., with a pH. of 8.8 (type: no. Y18). The eruption of Spray Geyser is regular and almost continuous; Imperial Geyser is no longer eruptive but it discharges a large volume of water; the habitats of the plant are rather uniform as a result. The corded masses of *Thalpophila* almost filled the channels of the streams on one visit to the region, and one could have collected several liters in a few minutes.

MASTIGOCLADACEAE Geitler

Synopt. Darst. Cyan., Beih. Bot. Centralbl., pt. 2, p. 41, 1925.

A single Yellowstone genus.

MASTIGOCLADUS Cohn

Alg. Karlsb. Sprudels, Abh. Schles. Ges. vaterl. Cultur 2, p. 39, 1863.

Filaments monosiphonous, typically dorsiventrally specialized, with long, slender (false) branches; "V"-branching present but mostly indistinctly shown and often obscured so that it resembles true branching or single normal false branching; branches abruptly arising from the main filaments, single or in pairs. Sheaths thin and firm or gelatinized and slimy. Heterocysts intercalary. Hormogonia unknown.

Type species: *Mastigocladus laminosus* Cohn.

In spite of the several attempts by various authors (Dickie, Schmidle, Tilden) to increase the number of species, *Mastigocladus* remains a monotypic genus. The plant is unique and, while not always easily recognized, is unmistakable after one becomes acquainted with it.

The single species is typically thermal and is cosmopolitan. It is the best-known single thermal plant and has been found in most important thermal spring groups. Its known range includes all the continents except the Antarctic.

KEY TO THE YELLOWSTONE SPECIES AND VARIETIES.

I. Filaments branched. *M. laminosus* 1.
II. Filaments unbranched.
    1. Heterocysts present. *M. laminosus* var. *anabaenoides* 1A
    2. Heterocysts absent. *M. laminosus* var. *phormidioides* 1B

1. MASTIGOCLADUS LAMINOSUS Cohn

Alg. Karlsb. Sprudels, Abh. Schles. Ges. vaterl. Cultur 2, p. 39, 1863.

Syn.: *Hapalosiphon laminosus* (Kütz.) Hansg., Bot. Centralbl., p. 48, 1885.
    Hapalosiphon laminosus Hansg., Bot. Centralbl., p. 48, 1885.
    Cyanothrix vaginata Schmidle, Allg. Bot. Ztg., p. 37, 1897.
    Hapalosiphon major Tilden, Amer. Algae, no. 167, 1896.

Stratum membranous to leathery, often lamellate, often with granules of lime especially in the underlying portions, firm and gelatinous to cartilaginous or spongy, dull blue-green to olive-green. Filaments thickly interwoven, $4-10\mu$ (usually $4-6\mu$) in diameter, contorted or often more or less flexuous, constricted or less often not constricted at the cross walls, cylindrical or in older filaments moniliform. Sheaths thin, distinct at first, later indistinct, slimy. Cells of the main filaments spherical, ovoid, barrel-shaped, or short cylindrical; cells of the branches ovoid to cylindrical, often very long cylindrical. Heterocysts intercalary, spherical to elliptical or short cylindrical, up to 7μ in diameter by up to 9μ in length, single or rarely in pairs.

M. laminosus is a cosmopolitan thermal alga. Geitler (1931) states that it has been found only three times in non-thermal waters: in a

brook in the Celebes; in the Rhein, Germany; and in Normandy, France. It has been found in numerous European, Asiatic, and African hot springs; in a few South American springs; in at least one Australian spring; in springs on several islands, including Iceland, New Zealand,

Fig. 40.—*Mastigocladus laminosus* Cohn, filament with "V" branching (×700).

and Tasmania. In North America it has been found in California at the Arrowhead Hot Springs near San Bernardino by Setchell (1899) at 49–50° C.; in Oregon in a hot spring in the Cascade Mountains by Lloyd (1895) at 55° C. (reported as *Hapalosiphon major* Tilden); and in Wyoming in the Yellowstone by Tilden (1896) at 54° C., and from 51° C. to 61° C. (?) (reported as *Hapalosiphon major* Tilden). The

Yellowstone spring in which Tilden found the alga is on a mountain near the Lower Geyser Basin.

I regard *Hapalosiphon major* Tilden as quite typical and not over-sized *M. laminosus*. The cell size is especially variable in old strata of *M. laminosus* and often the cell size comes close to the measurements cited by Tilden. The absence of crystals of lime (noted by her) in the Yellowstone material seems to me to be of no taxonomic significance and I should hesitate to place as a new species rather typical material of a well-known and known to be variable form on such grounds.

In the present investigation the plant has been found to be abundant and widespread in the Yellowstone. It has been noted in the Upper Geyser Basin: Bijah Geyser (no. 439), Mastiff Geyser (no. 440), Fire-hole River (nos. 441, 442), Chromatic Spring, and elsewhere; Lower Geyser Basin: Jelly Spring, and in five unnamed springs; Twin Buttes Region: Spray Geyser; West Thumb; several unnamed springs; Mam-moth Hot Springs: rare in several springs; and in many springs out-side of the major groups. It inhabited water at temperatures from $28.6°$ C. to $55.8°$ C., at acidities from pH. 6.8 to 9.0.

Lowenthal (1903) studied the plant in pure culture and stated that its upper temperature limit (experimentally) was $52°$ C. This point is exceeded in nature in several places in the Yellowstone.

1A. MASTIGOCLADUS LAMINOSUS Cohn

var. **anabaenoides** (Boye Petersen), comb nov.

Syn.: *Aulosira thermalis* G. S. West, Journ. of Bot. 40, p. 244, 1902.
      Hapalosiphon laminosum Hansg. f. *anabaenoides* Boye Petersen, Freshw. Alg. Iceland. Bot. of Iceland 2, p. 309, 1923.

Stratum brilliant blue-green, flocculent to soft spongy and friable, indefinite. Filaments unbranched, similar throughout; with barrel shaped to almost spherical cells and heterocysts. Trichomes thicker in the middle than at the ends. Filaments flexuous to spirally rolled, or almost straight. Sheaths thin, firm to slimy.

Boye Petersen described the plant as the forma *anabaenoides* rather than as a variety. His material was secured from hot springs in Iceland. In the Yellowstone *M. laminosus* and its var. *anabaenoides* have been found mostly in separate springs, and so no evidence was secured to indi-cate that the two are growth stages of a single plant. On the other hand, they have been found, in a few sites, growing intermixed, elim-inating their being ecological forms of the same species. Consequently, in opposition to Boye-Petersen's treatment, I am considering *anabae-noides* as a variety.

The occurrence of this plant is quite different from that of *M. laminosus*. It is in general less common, and reaches its greatest development in quite acid waters (while *M. laminosus* is found in basic or neutral waters). It has been noted in the Upper Geyser Basin: Bijou and Catfish Geysers (nos. 444, 445) at 34.9° C. and 35° C., pH. 8.55, rare; Twin Buttes Region: Spray Geyser (no. 428) at 33.1° C., pH. 8.85, occasional; Meadow Springs (nos. 186, 193) at 62.2° C. and 58° C., pH. 5.4, frequent to dominant; Mud Volcano Group: mud spring (no. 63) at 42.5° C., pH. 5.0, dominant. In the Mud Volcano Group of Springs this plant is the most abundant alga and, with *Pluto caldarius* (Tilden) and *Zygnema* sp., is one of the three important algae. It occurs most commonly on damp mud and in very shallow pools and rills. Above the larger of the several springs immediately south of the Mud Volcano there was for four years a growth of almost pure *M. laminosus anabaenoides* covering about one hundred square feet.

1B. MASTIGOCLADUS LAMINOSUS Cohn

var. **phormidioides** (Boye Petersen), comb. nov.

Syn.: *Hapalosiphon laminosum* Hansg. f. *phormidioides* Boye Petersen, Freshw. Alg. Iceland. Bot. of Iceland 2, p. 309, 1923.

Filaments unbranched, straight or spirally rolled, without heterocysts, not at all or very slightly tapering. Sheaths soft and slimy and partially or completely confluent; often invisible.

This variety was described as a form rather than as a variety by Boye Petersen. For reasons similar to those given under var. *anabaenoides* I regard this plant as a valid variety. The plant was described from hot springs in Iceland.

Found but twice in the Yellowstone, little can be concluded about its range. It has been noted in the Upper Geyser Basin: Catfish Geyser (no. 445) at 34.9° C., pH. 8.55, along with *M. laminosus* and the var. *anabaenoides;* Meadow Springs (no. 193) at 62.2° C. and pH. 5.4, with *M. laminosus anabaenoides.*

SCYTONEMATACEAE Rabenhorst

Fl. Eur. Alg. II, p. 246, 1865.

KEY TO THE YELLOWSTONE GENERA

I. Heterocysts present.	
1. False branches mostly in pairs.	SCYTONEMA (p. 93)
2. False branches mostly single.	TOLYPOTHRIX (p. 97)
II. Heterocysts absent.	PLECTONEMA (p. 100)

SCYTONEMA Agardh

Syst. Algar., p. 28, 1824.

Filaments scattered or more frequently united into a stratum, free but often in bundles; straight, flexuous, or contorted, with main filaments more or less prostrate and branches more or less erect, or less often without definite orientation. False branching mostly with branches in pairs, but in erect branches often single; paired branches divergent, parallel or crossing over; branching often at considerable distances from heterocysts and with no relationship to them, sometimes in erect filaments at heterocysts. Sheaths firm, lamellate with parallel or moderately divergent lamellae; colorless or yellowish. Trichomes with apical meristems of shorter and usually swollen cells; and intercalary meristems at points of branching with poorly differentiated structure. Heterocysts intercalary (or in tips isolated by single branching, basal). Hormogonia produced at ends of filaments. Resting cells absent.

Scytonema includes many species, the majority in fresh water or on damp soil, rocks, etc., a few marine, and several in thermal situations. *S. caldarium* Setchell is known from hot springs in California and India at temperatures of 27° C. and thereabouts; *S. azureum* Tilden is reported from Hawaii at 31° C.; *S. mirabile* var. *Leprieurii* (Mont.) Born. & Flah. from warm sulphur springs at Banff, Canada, and elsewhere; *S. mirabile* (Dillw.) Born. from the edge of a geyser in Iceland; *S. hyalinum* Gardner from a spring in Fukien Province, China; and *S. varium* Kütz. from many springs in Europe, Africa, and Asia. Several of these species occur also in non-thermal sites.

In the Yellowstone three species and a variety occur. Although locally important (Biscuit Basin, Chocolate Pots, and Firehole Lake section of Lower Geyser Basin) the genus is generally insignificant. The species occur in the cooler waters, substituting for the ecologically similar species of *Calothrix*. They are best represented in waters at from 20°C. to 40° C.

KEY TO THE YELLOWSTONE SPECIES

I. Trichomes 8–9μ in diameter.   *S. caldarium* 1.

II. Trichomes up to 5.5μ in diameter.

     1. Trichomes 3–5.5μ in diameter; strata spongy, not zoned.

         A. Sheaths uniformly pigmented, with lightly divergent lamellae.

                                         S. caldarium var. *terrestre* 1A.

         B. Sheaths with a lighter colored or colorless outer layer, with parallel lamellae.   *S. planum* 2.

     2. Trichomes 1.8–2.8μ in diameter; stratum stony and zoned.

                                         S. induratum 3.

1. SCYTONEMA CALDARIUM Setchell
Erythea 7, p. 48, 1899.

Stratum flocculent, extended; or poorly developed. Filaments in the basal part more or less prostrate and tangled, up to 16μ in diameter. False branches in pairs or in erect filaments often single, mostly erect, often in *Symploca*-like fascicles, or mostly free, 12–16μ in diameter. Cells 8–9μ (4–8μ?) in diameter, 2–3 diameters in length except in meristems, in meristems 0.3–0.6 diameters; cell contents olive-green to blue-green. Heterocysts discoidal to short cylindrical, 0.6–2.0 diameters in length. Sheaths firm, with parallel lamellae, colorless in younger filaments, golden brown in older filaments or parts.

Geitler (1932), upon examining Setchell's material, found the cells to be 8–9μ in diameter rather than 4–8μ as given by Setchell. I agree with Geitler in this respect, and also find the stratal characters to be less constant than indicated by Setchell.
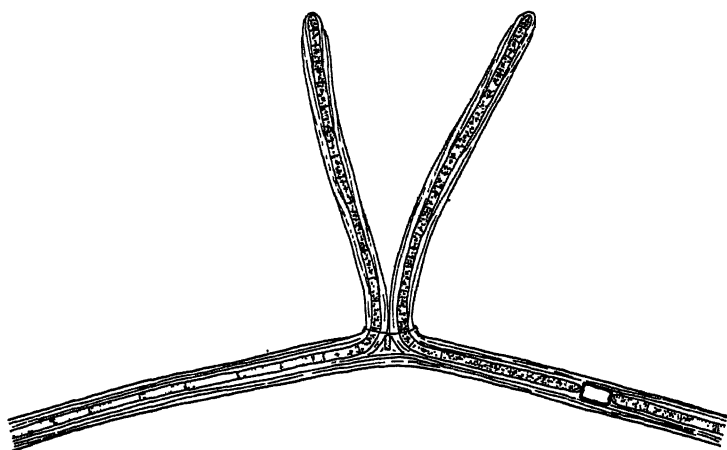
FIG. 41.—*Scytonema caldarium* var. *terrestre*, filament with young paired branches (×375).

Described from Waterman Hot Springs, near San Bernardino, California, the plant grew on rocks kept wet by water at 27° C. It has since been noted in India. Its presence in the Yellowstone has not previously been noted.

It has been found in the Yellowstone a single time, in one of the Chocolate Pots (Iron Springs) of the Gibbon Canyon, growing at 29.4° C., and pH. 6.4 (no. 280), growing with *S. planum* (of this paper).

1A. SCYTONEMA CALDARIUM Setchell
var. **terrestre**, var. nov.

Stratum extended, spongy and tough, up to 8 mm. in thickness (usually about 5 mm.), dark blue-green to olive-blue-green, growing on warm damp soil and

rock. Filaments below more or less horizontal and somewhat contorted, above more or less erect and flexuous to straight, agglutinated above into erect tufts up to 2 mm. in height. Filaments long, 8–12μ in diameter, branching abundantly; branches mostly in pairs, in the erect filaments often single. Sheaths firm, thick, smooth, hyaline to pale yellowish or golden brown, with often indistinct, lightly divergent lamellae. Trichomes 3–5μ in diameter (mostly 4–5μ), usually slightly swollen at tips, not constricted at the cross walls (except in the meristems). Cells up to 4 diameters in length and mostly 2.5–3.5 diameters (shorter in the meristems). Cell contents mostly granular. Heterocysts 4.4–6.0μ in diameter by 6–15μ in length (mostly 10–13μ).
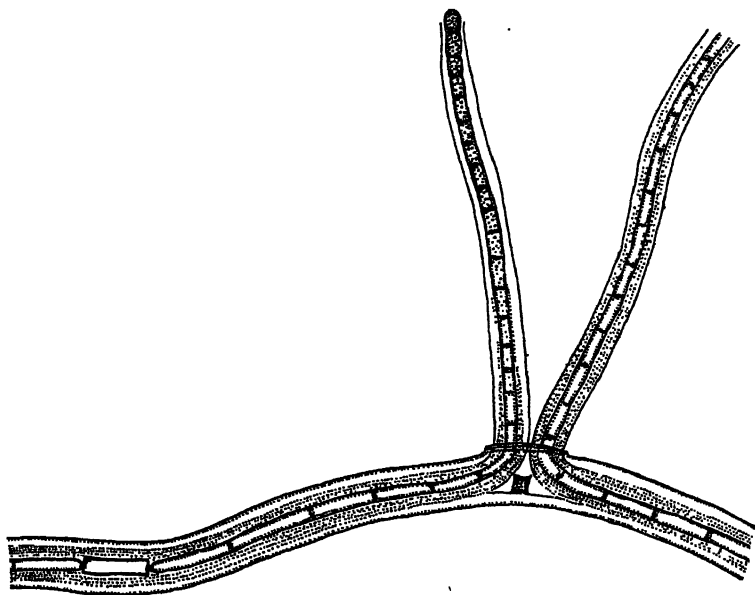
FIG. 42.—*Scytonema planum*, filament with young paired branches (×400).

The smaller diameter of the filaments and trichomes, the longer cells, the divergent lamellae, and the terrestrial habitat of this variety separate it from *S. caldarium* Setchell. The distinction is quite sharp, since, according to Geitler (1932), Setchell's material had trichomes 8–9μ in diameter (rather than 4–8μ, as stated by Setchell).

S. caldarium terrestre is locally quite abundant on the edges of the Firehole Lake, Lower Geyser Basin. It has not been found elsewhere. It inhabits wet, warm soil and rock; its known latitude in temperature is from 26.5° C. to 37.8° C. The type (no. 402) was growing at 32.2° C.

2. Scytonema planum, sp. nov.

Stratum extended, tough spongy, up to 3 mm. in thickness, dull rusty brown to blackish in color. often somewhat indurated with iron salts; surface even and plane, or rarely somewhat papillate.   Filaments 14–20μ in diameter (mostly cir. 16μ), tips of filaments 9–10μ in diameter (sheaths thinner), loosely interwoven and flexuous to somewhat contorted, without regularity of arrangement; false branches mostly in pairs, occasionally single in erect filaments, of the same size as the main filaments except when very young. Sheaths golden brown, with a thick, pale yellow or colorless coating, pigmented inner portion feebly lamellate, outer portion homogeneous, lamellae parallel, apices of filaments with colorless sheaths, surface of sheaths even and regular.   Trichomes 3.0–3.5μ in diameter, at apices cir. 4μ in diameter.   Cells cylindrical, 3–5 diameters in length. shorter in apical regions and 0.7–1.5 diameters, not constricted at cross walls except at tips; cell contents blue-green.   Heterocysts occasional, solitary, without relationship to branches, cylindrical, 5.5–6.0μ in diameter by 12–18μ in length.   Hormogonia unknown

Resembling *S. caldarium* Setchell, *S. caldarium terrestre* (of this paper), and *S. longiarticulatum* Setchell in several respects, this species is, nevertheless, easily distinguished.   From the first species and its variety it may be separated by its longer cells, longer heterocysts, thicker sheaths, and conspicuous pale outer layer of the sheaths of mature filaments.   From the latter species it is to be distinguished by its more slender trichomes, thicker sheaths, and well-developed stratum.   It resembles *S. caldarium* and its var. *terrestre* in the well-developed strata, general conformation, and habit; it accords with *S. longiarticulatum* in having elongate cells and a lighter outer layer around the sheaths.

It is abundant at the Chocolate Pots (Iron Springs) in the Gibbon Canyon. growing on the wet sides of the cones and in shallow water or on wet rock at their bases.   It has not been noted elsewhere.   At this site it grew at temperatures from 23° C. to 42° C., at pH. 6.05–6.6.   The type (no. 280) was at 29.4° C. and pH. 6.4.   It was growing with *S. caldarium* Setchell and *Chroococcus minutus* (Kütz.) Naeg.

3. Scytonema induratum, sp. nov.

Stratum extended, up to 1 cm. in thickness or more, rich brown in color, hard and stony, heavily indurated with silica and paler in lower portions, horizontally zoned with layers 0.5–3.0 mm. thick, vertically fibrous, very smooth above.   Filaments with false branching, the branches in pairs and similar to the main filament, mostly erect and more or less parallel except in basal parts, there tangled and somewhat prostrate. uniformly cylindrical.   Sheaths yellowish-brown except at tips of rapidly growing filaments, lamellate with feebly divergent lamellae, thick, firm. often fragile, covered with a crystalline, colorless to whitish layer of silica 2–8μ thick; filaments with jacket of silica 13–22μ

(mostly cir. 17μ) in diameter, without jacket 7–9μ in thickness; due to irregular coating filaments often uneven. Trichomes 1.8–2.8μ in diameter, cylindrical, swollen at apices and up to 3.5μ. Cells 8–12 diameters in length, cylindrical, not constricted at cross walls; cell contents mostly homogeneous, with infrequent granules. Heterocysts intercalary, infrequent, cylindrical, and usually swollen, cir. 3μ in diameter by 5μ in length. Branching infrequent. Hormogonia unknown.

This species is quite distinct. The heavy incrustation causes it to be very difficult to work with, and the strata are easily passed by since they give little evidence of being alive. One can walk over the plant with heavy shoes and leave no footprints or impressions on the surface. Collecting the plant requires sturdy implements; a chisel and hammer are needed.

FIG. 43.—*Scytonema induratum,* portion of filament, incrusted with silica ($\times$540).

In the Biscuit Basin this is the most important species in general. It covers much of the wet sinter and one bed of it covered almost half an acre. It was found at 21–46.6° C., and pH. 8.8–9.05. The type (no. 371) came from a site that had a fluctuating temperature, varying from 27° C. to 37° C., and a pH. of 9.0. This was in the overflow of Sapphire Geyser. The plant occurs also in Jewel Geyser overflow and in the wet pools throughout the basin.

TOLYPOTHRIX Kützing

Phyc. gen., p. 227, 1843.

Filaments mostly united into tufts or more or less definite strata, either attached or free-floating; with false branches mostly single, infrequently also in pairs. Filaments erect or prostrate, usually free. Branches arising below a heterocyst, of the same size and nature as the main filament. Trichomes usually with apical meristems, which have shorter and swollen cells. Heterocysts intercalary (or basal by breakage). Hormogonia at ends of filaments. Resting cells mostly absent.

The many species occur chiefly in fresh water and on damp soil, rocks, tree trunks, etc. A single species is thermal. This one, *T. curta* Gardner, is known from a hot spring in Fukien Province, China.

The genus is of little importance in the Yellowstone.

I. Free living, with normal branching; filaments in strata or tufts.
  1. Tufts (or plant mass) up to 3 cm. in length.   *T. distorta* 1.
  2. Tufts 5 cm. or greater in length.   *T. distorta* var. *penicillata* 1A.
II. Endophytic, with suppressed branching; filaments single.
                                        T. distorta var. *endophytica* 1B.

1. TOLYPOTHRIX DISTORTA Kützing

Phyc. gen., p. 228, 1843.

Stratum tufted and turf-like, cushion-like or caespitose-flocculent, blue-green
to brown, often incrusted with lime. Filaments flexuous, abundantly branched,
up to 3 cm. in length, 10–15μ in diameter, with obliquely divergent branches.
Sheaths firm, thin, at first colorless, later yellowish to brown, often inflated at
branch bases. Cells 9–12μ in diameter, quadrate or shorter than their diam-
eters, lightly constricted at the cross walls; cell contents blue-green. Hetero-
cysts single or in rows of 2 or 3, spheroidal to quadrate or short-cylindrical.
End cells usually somewhat flattened.

This widely distributed species occurs in standing or flowing fresh
water. It is known from numerous localities in North America, but has
not been previously reported from the Yellowstone.

Generally abundant in quiet non-thermal waters in the Park, it has
been found in some 18 sites. It has been encountered a single time in
slightly warm water in the Firehole River opposite the Biscuit Basin
(nos. 431, 432, 433), at 22.5° C. and pH. 8.2. The species is clearly
non-thermal.

1A. TOLYPOTHRIX DISTORTA Kützing

var. PENICILLATA (Ag.) Lemm.

Krypt.-Fl. Mark Brand. 3, p. 218, 1910.

Plant mass penicillate-caespitose, or cushion-like with free tufts, blue-green
to brown, several centimeters long. Filaments abundantly branched, very long,
8–17μ in diameter, with more or less ascending and parallel branches. Sheaths
thin or thickish, colorless at first, later brown. Cells cir. 10μ in diameter and
4–13μ in length, shorter or slightly longer than their diameters, often slightly
swollen, lightly constricted at the cross walls, blue-green to olive-green. Hetero-
cysts single or in rows of 2–4, often infrequent. End cells almost spherical.

Widespread in flowing streams and in the littoral zone of lakes, this
variety is not very well known in North America. It has been reported
by Farlow from New Hampshire and by Austin from New Jersey (?).

In the Yellowstone it is less abundant than *T. distorta,* but common.
It occurs in (as far as noted) most of the larger streams. It was found,

along with *T. distorta,* in the Firehole River opposite the Biscuit Basin (no. 433) in slightly warmed water at 22.5° C. and pH. 8.2. Elsewhere it was in completely non-thermal waters.

1B. Tolypothrix distorta Kützing

var. endophytica, var. nov.

Filaments endophytic in *Nostoc,* short, straight, rigid, unbranched, 11-15μ in diameter by 60–200μ in length. Sheaths thin, homogeneous colorless or rarely yellowish. Cells 9–12μ in diameter, quadrate or shorter than long, slightly swollen; lightly constricted at cross walls, cell contents blue-green. Heterocysts single, basal, hemispherical to spherical, rarely intercalary. End cells almost spherical.

Fig. 44.—*Tolypothrix distorta* var. *endophytica* ($\times$650).

The var. *endophytica* superficially gives little evidence of being a *Tolypothrix.* It lacks the characteristic features of *T. distorta* as well, as far as its gross appearance is concerned. The filaments fragment as intercalary heterocysts differentiate, and so there is no opportunity for branching. However, the filaments regularly lie imbedded in the *Nostoc* in such a position that they show, in carefully made preparations, a relationship that must be interpreted as due to a modified false branching. The dimensions, cellular structure, and aspect are clearly those of *Tolypothrix,* and in particular are those of *T. distorta* or its var. *penicillata.*

The plant has been found in a single site only, in the Firehole River at the Biscuit Basin, growing in *Nostoc verrucosum* (L.) Vauch., at 22.5° C., and pH. 8.2 (type: no. 432).

PLECTONEMA Thuret

Essai class. Nost., p. 375, 1875.

Filaments either solitary or forming a definite stratum, prostrate or erect, and with false branching; branches single or in pairs, the pairs emerging from the sheath on the same side of the filament, or the two on opposite sides, parallel, divergent, or crossing over near their origin. Hormogonia usually present; heterocysts absent; resting cells absent. Trichomes cylindrical, occasionally swollen at tips.

The taxonomic position of *Plectonema* is puzzling. Its lack of heterocysts and general microscopic appearance tend to ally it with the Oscillatoriaceae, close to *Lyngbya*. On the other hand, its branching is of the type found generally in the Scytonemataceae, especially in *Scytonema*, several species of which have the branches either single or in pairs.

Of the some thirty species of *Plectonema* only one, *P. yellowstonense* Prát, has up to the present been found in thermal waters. Of the others a few (five) are typically marine, many fresh water, and a few terrestrial. The genus is wide-spread and includes several cosmopolitan species.

KEY TO THE YELLOWSTONE SPECIES

I. Cells 1–2 diameters in length; sheath soft, uneven, swollen in places.
P. yellowstonense 1.
II. Cells 2–6 diameters in length; sheath firm, cylindrical, even.
P. Dangeardii 2.

1. PLECTONEMA YELLOWSTONENSE Prát

Studie o Biolithogenesi, V Pr., Nák. České Ak. v. a Um., p. 99, 1929.

Filaments growing in the slime incrustation of Chara, straight to spirally or irregularly twisted or contorted; stratum indefinite, filaments sparsely scattered through the incrustation of lime; false branches single or in pairs. Sheaths colorless, invisible without staining, with surface in part smooth, in part irregularly swollen, at the apices closed and pointed or open and funnel-shaped. Trichomes crooked, mostly cir. 1μ in diameter (less often up to 2–3μ); without constrictions at the cross walls but with the cells in places swollen and barrel-shaped. Cells 1–2 diameters in length.

According to Prát, who studied the organism in pure culture, it forms slimy to mucilaginous tufts, varying in color from reddish olive-green to yellowish olive-green, dull brownish or golden brown.

The species was described by Prát from warm water near Jupiter Terrace, Mammoth Hot Springs, Yellowstone. *Chara* is quite abundant in the cooler waters of the main rill from Jupiter Terrace and associated springs, and in the warm marsh below the terraces. The *Chara* appears to be confined to waters with a temperature below 40° C. in the Mammoth region, and it is reasonable to assume that *P. yellowstonense* grew between 20° C. and 40° C.

In the present investigation the plant has been found twice in the marsh below Jupiter Terrace, on *Chara* at temperatures of 23° C. and 29.9° C., and once on *Vaucheria* at 29.8° C., in each case at cir. pH. 8.0. As an epiphyte on green algae it appears to be limited to tepid water.

2. PLECTONEMA DANGEARDII Frémy

Myx. d'Afr. équat., Arch. de Bot. 3, p. 175, 1930.

Filaments single or in groups of a few, almost straight, 2.5μ in diameter, richly false-branching. Branches mostly in pairs, less often single, erect or divergent. Sheaths hyaline, firm, smooth, even. Trichome pale blue-green, not constricted at the cross walls, 1.5μ in diameter. Cells 2–6 diameters in length, $3–9\mu$ long, not granulated at the cross walls. End cells rounded, without calyptra.

Frémy described the species from standing and slowly flowing water in French equatorial Africa. Its presence elsewhere has not been noted.

In the Yellowstone, the alga is a rare component of the *Scytonema-Stigonema-Schizothrix* beds in the Firehole Lake section of the Lower Geyser Basin. Interestingly, it is found mostly as a terrestrial rather than a strictly aquatic form, although it occurs in quite wet places. Its temperature range, as observed, was from 17–39° C. It was most abundant at 34° C. on the banks of the Firehole Lake.

HAMMATOIDEACEAE Elenkin

Journ. d. Russ. Bot. Ges. 1, 1916

Syn.: Tildeniaceae Kossinskaja, Not. syst. Crypt. Horti Bot. Princ. U. S. S. R. 4, p. 85, pl. 2, f. 1–14, 1926.

Trichomes monosiphonous, simple, unbranched. Filaments with false branching, singly or in pairs, differentiated into more or less prostrate basal filaments without base apical differentiation, and more or less erect branches. Branches at least in part tapering and often bearing colorless hairs. Ends of the pros-

trate filaments may be bent up and assume the characters of the branches. Growth intercalary, apical or trichothallic, often all types present in a single species. Sheaths firm or soft, often lamellate and often with distinctly flaring lamellae. Heterocysts present or absent. Resting cells present or absent. Hormogonia present.

The family Hammatoideaceae encroaches rather closely on both the Scytonemataceae and the Rivulariaceae. It is essentially a group of species that fit equally well, or rather that do not fit at all, in either family. The genera I am including in this family are *Tildenia** Kossinskaja (1926), *Scytonematopsis* Kisselewa (1930), and *Hammatoidea* W. & G. S. West (1897). West (1897, etc.) placed *Hammatoidea* in the family Camptotrichaceae, along with *Camptothrix* W. & G. S. West. Elenkin (1916) formed for *Hammatoidea* a separate family, the Hammatoidaceae. Kossinskaja (1926) made *Tildenia* the type and only genus of the family Tildeniaceae. Kisselewa (1930) allied *Scytonematopsis* with *Tildenia*. Geitler (1931, 1932) recognized the three genera, but was doubtful of the distinction between *Tildenia* and *Scytonematopsis*. He placed these genera in the Scytonemataceae, and *Hammatoidea* in the Rivulariaceae. I am following Geitler (1925, 1931) in separating *Hammatoidea* from *Camptothrix;* and I consider *Tildenia** and *Scytonematopsis* to be synonymous. The relationships of the individual genera will be considered below.

<div align="center">KEY TO THE YELLOWSTONE GENERA</div>

I. Heterocysts present.	SCYTONEMATOPSIS (p. 102)
II. Heterocysts absent.	HAMMATOIDEA (p. 105)

<div align="center">SCYTONEMATOPSIS Kisselewa</div>

<div align="center">Journ. Russ. Bot. Ges. 15, p. 174, 1930.</div>

Syn.: TILDENIA Kossinskaja, Not. syst. Inst. Crypt. Horti. Bot. Princ. U. S. S. R. 4, p. 85, 1926. Not TILDENIA Miq. 1842.

Filaments free or aggregated into bundles, tapering at one or both ends, of two sorts: prostrate with false branches mostly in pairs and with intercalary or apical meristems; and more or less erect with tips attenuated into distinct hairs or tapering, with usually trichothallic growth, or some regularly cylindrical with apical meristems, and with false branches mostly single. False branches when in pairs parallel or divergent, originating at heterocysts or not; when single originating at heterocysts. Sheaths firm, homogeneous or lamellate with parallel or divergent lamellae. hyaline or yellowish to brown. Heterocysts intercalary and basal. Hormogonia either at the ends or bases of the trichomes. Resting cells present or absent.

* *Tildenia* is preoccupied by the use of that name by Miquel in 1842 for a group of vascular plants and so cannot be revived as a genus of Myxophyceae.

Type species: **Scytonematopsis fuliginosa** (Tilden) comb. nov.

In the general habit of growth *Scytonematopsis* resembles *Scytonema* quite closely. The apical meristems with swollen short cells are quite characteristic of several genera of the Scytonemataceae and it seems unjustifiable to transfer the species of Scytonematopsis to the Rivulariaceae because of the tapering and hairbearing trichomes. *S. fuliginosa,* from the descriptions, does not have the apical meristems, there is no mention of the location of the meristematic regions.

The only species credited to the genus, up to the present, are *S. fuliginosa,* found by Tilden in a shallow tide pool in Hawaii (it was described as *Scytonema f.* Tild.), and *S. Woronichinii* Kiss., described from Samarkand (Turkestan). The genus has not previously been reported from North America.

A single Yellowstone species.

1. Scytonematopsis hydnoides, sp. nov.

Stratum extensive, up to 2 cm. in thickness, soft-cartilaginous, vertically fibrous, often feebly incrusted with silica, bearing on the upper surface erect, hydnoid, weakly anastomosing fascicles up to 8 mm. in height, brilliant blue-green throughout or somewhat paler below and slightly yellowed; or forming a blue-green to olive-green, gelatinous, entangled, and corded attached mass. Main filaments prostrate and more or less tangled and contorted, sometimes semi-erect, with false branches emerging in pairs and usually more or less erect and parallel or gradually divergent; the erect branches feebly entangled and mostly parallel, with false branches emerging singly below heterocysts, the secondary branches erect or soon becoming so. Tips from the erect branches frequently break off and become independent plants. Distinction between main filaments and branches not constant. Filaments and branches cylindrical for the most part, often slightly swollen toward the basal ends, and at the distal ends either swollen slightly and meristematic or tapering into a rather long, distinct, colorless hair, which extends well beyond the sheath. Filaments very long, up to 2 cm. or more; main filaments 13–22μ in diameter, branches 10–15μ in diameter. Sheaths firm and soft but never slimy, moderately thick, distinctly lamellate with parallel or feebly divergent lamellae, hyaline in young filaments, becoming golden yellow in older ones, at the apices open, funnelshaped, with flaring "hair-like" lamellae. Trichomes 5–10μ in diameter in basal filaments, 5–7μ in diameter in erect branches, tapering down to 2.5–3.5μ in hairs, more or less constricted at the cross walls, especially in the meristematic regions, less constricted to cylindrical in non-meristematic portions of branches. Cells blue-green to olive-green, usually with a few to many small but distinct granules, and with 0–4 (usually 1) distinct and large refractile granules, 2–4 diameters in length in non-meristematic regions, down to 0.5 diameter in meristems, and 2–4 diameters in hairs. Heterocysts intercalary and basal (originating as intercalary before branching at that point), intercalary heterocysts not at branches single and cylindrical, often swollen, 5–15μ
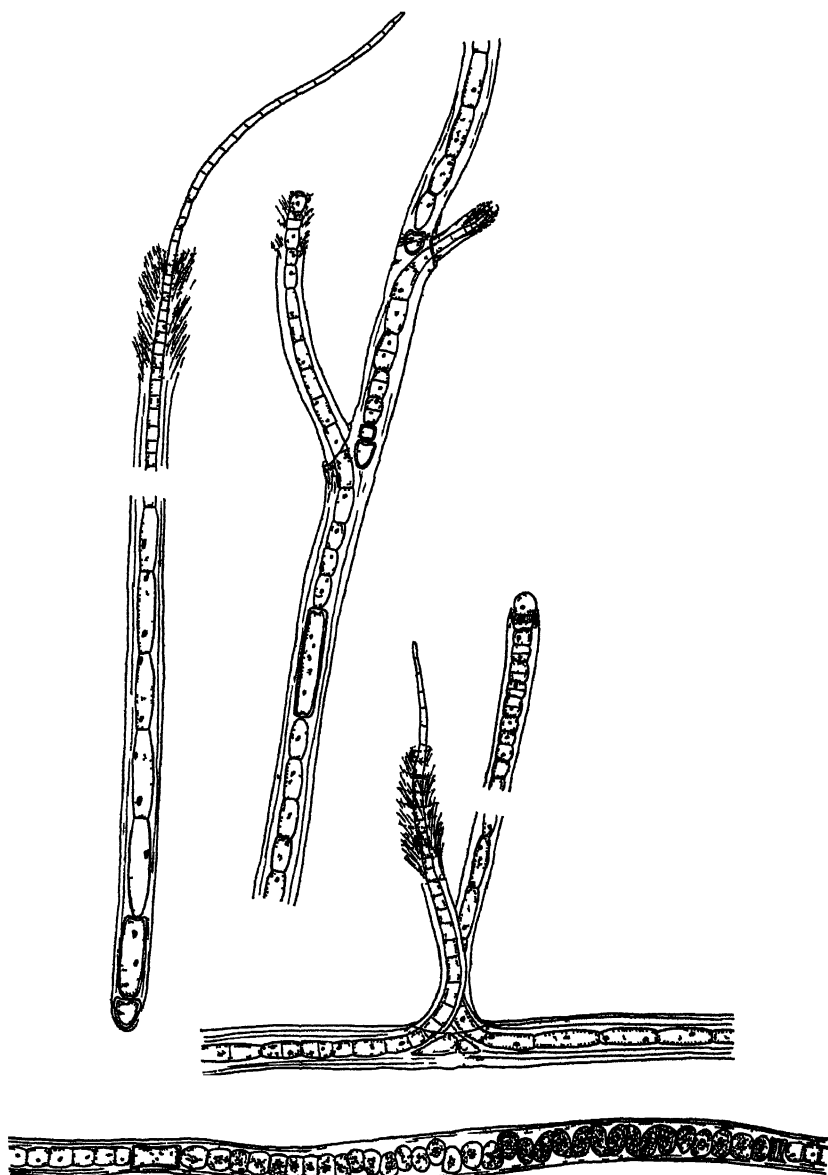
FIG 45 —*Scytonemaptosis hydnoides*, left, detached branch with aspect of *Calothrix* (×400) ; center, erect filament with single false branching (×350) ; right, prostrate filament with paired false branching (×350) ; below, old filament with numerous resting cells (×350).

in diameter by 20–90μ in length; branch (and basal) heterocysts single or in rows of 2 or 3, spherical, hemispherical, or almost quadrate, 7–11μ in diameter by 8–13μ in length, or rarely smaller. Resting cells usually in contorted rows of up to 150, in the older filaments, 6–9μ in diameter by 5–10μ in length, membranes smooth. Hormogonia poorly developed, basal; reproduction by fragmentation as well as by hormogonia and resting cells.

S. hydnoides is a sharply distinct species. Its relationship to *S. fuliginosa* is not close, and it is very distinct from *S. Woronichinii* Kiss.

The plant has been collected in the greatest abundance in a small pool between Oblong and Giant Geysers, Upper Basin, where it grew (type: no. 445) at 34.9° C. and pH. 8.55, and on the spray-washed sinter edge of the same pool (no. 444), at a similar alkalinity and temperature. It has also been observed in several other sites: Upper Basin: Beach Spring, Chromatic Pool, Beauty Pool, Sunset Lake; Twin Buttes Region: Spray Geyser overflow (no. 422, 55° C., pH. 8.75). The plant has been found only in quite alkaline waters.

HAMMATOIDEA W. & G. S. West

Jour. Roy. Micr. Soc., p. 407, 1897.

Filaments in tufts or in indefinite strata, often more or less prostrate with ascending branches and tips, or bent in the middle with ascending ends. Trichomes tapering at both ends, and bearing colorless hairs. False branches produced mostly in pairs, parallel or crossing over. Sheaths firm, lamellate. Heterocysts lacking. Resting cells unknown. Hormogonia present.

Type species: *Hammatoidea Normanni* W. & G. S. West.

The genus was formed to include the single species, *H. Normanni,* by West and West. Their species differs sharply from the one described below. The diagnosis of the genus has been modified to include a wider range of forms than their species alone. *Hammatoidea* shows marked similarities to *Scytonematopsis*—being separated from it chiefly by its lack of heterocysts. Both genera have in certain features the general habit of growth of species of *Scytonema*. *H. Normanni* is known from England, Poland, Chatham Island, and Greenland, in non-thermal waters.

The genus is unimportant in the Yellowstone.

A single Yellowstone species.

1. Hammatoidea yellowstonensis, sp. nov.

Filaments growing on the surface of gelatinous Myxophyceae, scattered or in small clumps, 5–7μ in diameter in middle by up to 500μ in length, tapering

gradually at both ends, with false branches in pairs, crossing over at base, more or less prostrate with tips and branches somewhat ascending, ending in long slender colorless hairs cir. 0.7μ in diameter. Trichomes straight, not constricted at the cross walls, $3–5\mu$ in diameter. Sheaths yellowish-brown, firm. lamellate with parallel lamellae, funnel-shaped and flaring at bases of hairs. Cells cylindrical, blue-green, 1.5–3.0 diameters in length, longer in the hairs, with granular cell contents. Hormogonia present. Heterocysts absent.
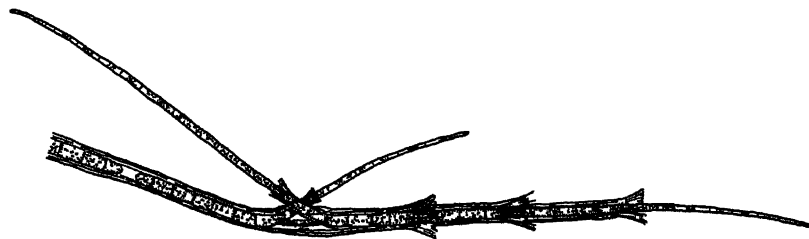
Fig. 46.—*Hammatoidea yellowstonensis,* apical portion of filament showing paired branches and tapering trichomes ($\times650$).

The dimensions, habitat, flaring ends of sheaths, cell shape, and position of filaments all separate this species from *H. Normanni.* The plant is distinctive.

It has been found only below Jupiter Terrace, Mammoth Hot Springs (type: no. 240), growing on various Myxophyceae: *Phormidium, Mastigocladus,* etc., at 30° C. and pH. 7.85. In this site it was common but not abundant.

<div align="center">RIVULARIACEAE Rabenhorst</div>

<div align="center">Fl. Eur. Alg., II, p. 2, 1865.</div>

<div align="center">KEY TO THE YELLOWSTONE GENERA</div>

I. Sheaths firm and mostly distinct, filaments not in a common matrix.
  1. Bases of branches enclosed in common sheath of the main filament; branches often in tufts.   DICHOTHRIX (p. 106)
  2. Bases of branches not in common sheath of the main filaments; branches mostly single.   CALOTHRIX (p. 108)
II. Sheaths more or less confluent; filaments in a common matrix.
  1. Resting cells present.   GLOEOTRICHIA (p. 124)
  2. Resting cells absent.   RIVULARIA (p. 126)

<div align="center">DICHOTHRIX Zanardini</div>

<div align="center">Plant. Maris rubri Enum., p. 89, 1858.</div>

Plants caespitose or penicillate, often in pulvinate strata. Filaments with false branching; bases of several of the false branches (two to six) inclosed

within the sheaths of the main filaments; branching often subdichotomous; filaments tapering from the usually swollen bases to the apices, frequently ending in colorless hairs. Main filaments regularly pushed to the side by the developing branches. Branches arising below the heterocysts. Heterocysts basal and at the bases of the branches, infrequently intercalary, in a single species absent. Hormogonia formed after the loss of the hairs. Resting cells unknown.

Type species: *Dichothrix penicillata* Zanardini.

The species of *Dichothrix* grow in fresh water, either running or standing, salt water and supersaline marshes, and in hot springs. Several are epiphytic or aquatic plants. *D. montana* was described by Tilden (collected by Griffiths) from hot water at Lo Lo, Montana. *D. compacta* Born. et Flah. has been found in hot springs in Europe (in Iceland at 55° C.). *D. gypsophila* (Kütz.) Born. et Flah. was reported by Weed (1889) and Tilden (1896) from the Yellowstone, growing in the overflow channels of geysers in the Upper Geyser Basin, and in Excelsior Geyser, Midway Geyser Basin. Weed's report is not illuminating. He stated that the sinter depositions (locally) were due "to the growth of the little alga—*Dichothrix gypsophila*—or its young form, *Mastigonema thermale.*" With his taxonomic outlook on the Rivulariaceae, any species of *Dichothrix, Calothrix,* et al. would have been included in the single species, and his record may, therefore, be disregarded. Tilden's report seems to be based chiefly on Weed's; to me her record is quite doubtful. Tilden's views on the identification of the various Rivulariaceae were somewhat more advanced but quite comparable to those of Weed. In another connection she explained her reasons for describing a new (thermal) species of *Dichothrix:* "Being very plainly a *Dichothrix,* it cannot be included under *Calothrix thermalis,* and is therefore made a new species." I am disregarding the Yellowstone records for *D. gypsophila* in the absence of authoritative information.

In the Yellowstone thermal springs the genus is not important.

KEY TO THE YELLOWSTONE SPECIES

I. Sheaths not lamellate; filaments 9–13.5μ in diameter.   *D. compacta* 1.
II. Sheaths lamellate; filaments 15μ in diameter or greater.   *D. Baueriana* 2.

1. DICHOTHRIX COMPACTA Born. & Flah.

Ann. Sci. Nat. Bot. 8, 3, p. 379, 1886.

Plants caespitose, often in tufted strata, filaments densely packed. Filaments up to 1 mm. long by 9–13.5μ in diameter. False branches erect, penicillate, appressed, often included in the sheath of the main filament for some distance. Sheaths lamellate, smooth, yellowish to brownish; above often dilated

and torn. Trichomes 4.2–6µ in diameter, ending in slender hairs. Cells 0.5–1.0 diameter in length, pale olivaceous to dull green. Heterocysts almost spherical or ovoid.

Growing in flowing and standing waters, on stones and other stable objects, or in hot springs, the species has been reported only once in the United States, at San Bernardino, California (Setchell). It has been found in Iceland in a hot spring at 55° C. There are no thermal records for it in the United States.

In the Yellowstone it has been found only in non-thermal waters. It was noted in the Little Firehole River near the Lower Geyser Basin at 19° C. and pH. 8.55, in water feebly warmed by thermal springs. It was found in greater abundance in the Gallatin Mountains near the source of Panther Creek; and on wet rocks in a mountain rill, along with *Hydrurus,* on the Teton Pass just south of the Yellowstone.

2. DICHOTHRIX BAUERIANA (Grun.) Born. & Flah.

Ann. Sci. Nat. Bot. 8, 3, p. 375, 1886.

Stratum extended, up to 1 cm. in thickness, green to brown; plants caespitose-penicillate. Filaments flexuous, 15–18µ (up to 21µ) in diameter. Sheaths close, gelatinous, homogeneous, colorless to yellowish. Trichomes 5–7.5µ, rarely up to 9µ in diameter, pale blue-green, tapering gradually into long hairs; sometimes but not regularly constricted at the cross walls. Cells 0.5–1.0 diameter in length. Heterocysts basal, spherical to hemispherical.

In the United States this plant has been noted in running and quiet water and on wet rocks (and on rocks in the littoral zone on the coast of Porto Rico). It appears to be widely distributed.

In the Yellowstone it has been noted a single time, in Spray Geyser overflow, Twin Buttes Region (no. 422) at 55° C., pH. 8.75. It formed occasional tufts in shallow water, growing on sinter rock.

CALOTHRIX Agardh

Syst. Alg., p. 24, 1824.

Filaments solitary, in tufts or clumps, or in extended and definite strata, often more or less parallel, mostly erect, unbranched or with false branching, branches usually single, rarely in pairs; filaments and trichomes frequently swollen at bases and tapering into more or less well-developed hairs at apices. Sheaths mostly firm, never confluent, often lamellate, often pigmented, or homogeneous and colorless. Heterocysts basal and sometimes also intercalary. Resting cells in some species, basal, single or in rows of a few. Hormogonia often in long rows.

The sixty or seventy species of this difficult genus inhabit a wide range of habitats: salt water (usually intertidal), fresh water, warm and hot water, and damp soil, rocks, and tree trunks. Several thermal species are widely distributed and abundant. The known thermal types include: *C. thermalis* (Schw.) Hansg., *C. Castellii* (Massal.) Born. & Flah., *C. africana* Schmidle, *C. epiphytica* W. & G. S. West, *C. Goetzei* Schmidle, *C. parietina* var. *thermalis* G. S. West, *C. calida* Richter, and *C. Kuntzei* Richter. The latter two were described from Yellowstone hot springs and *C. thermalis* has been reported from them. The first two were reported by Richter; the last by Tilden.

In the Yellowstone the twelve species encountered in this study comprise a very important group. They are characteristic of the cooler waters—below 55° C. and are most abundant from 20 to 40° C. Within this range in the majority of springs they (or one of them) are abundant and include active rock-depositing species. They seem to be of considerable importance in the formation of the hot spring terraces and cones. In general they are the most important components of the *Calothrix-Scytonema-Schizothrix* formations that cover large areas in the Lower Geyser Basin, and of the *Calothrix*-Diatom associations found generally in the basic, neutral and slightly acid springs. In extremely acid springs they are absent. Quite possibly *Calothrix* may be placed second to *Phormidium* in importance in the Yellowstone thermal springs, although other genera (*Oscillatoria, Synechococcus*) include more species and are as widely or more widely distributed.

The accurate determination of several species is not easy and many characters are variable and unreliable. Undoubtedly additional study will reveal several other species in the region.

<center>KEY TO THE YELLOWSTONE SPECIES</center>

I. Sheaths homogeneous; heterocysts basal only.
  1. Sheaths hyaline.
    A. Cells shorter than their diameter.   *C. Braunii* 1.
    B. Cells longer than their diameter.   *C. Geitleri* 2.
  2. Sheaths golden to yellowish, at least in the lower parts of mature filaments.   *C. charicola* 3.
II. Sheaths lamellate; heterocysts basal and intercalary or basal only.
  1. Sheaths hyaline; heterocysts basal only.   *C. fusca* 4.
  2. Sheaths yellowish or golden in at least the lower parts of mature filaments; heterocysts basal and intercalary.
    A. Sheaths with uniform pigmentation; without hyaline layer around pigmented portions of sheaths.
      a. Strata variable: felt-like, leathery, crustaceous, or of scattered tufts; strata less than 3 mm. in thickness.

    *. Filaments mostly branched; strata crustaceous, or with filaments in tufts.   *C. parietina* 5.

    **. Branching rare; strata felt-like or leathery.

       !. Filaments 8–10μ in diameter; stratum felt-like.

                                          C. thermalis 6.

       !!. Filaments 10–15μ in diameter; stratum leathery.

                                        C. coriacea 7.

  b. Strata pilose, 4 mm. or greater in thickness.

    *. Filaments 8–13μ in diameter.

       !. Intercalary heterocysts up to 7 diameters in length, often in series.   *C. Kuntzei* 8.

       !!. Intercalary heterocysts 2 diameters or less in length, never in series.   *C. calida* 9.

    **. Filaments 14–20μ in diameter.   *C. cavernarum* 10.

B. Sheaths with hyaline layer around pigmented portions.

  a. Sheaths golden, with hyaline outer layer, without hyaline inner layer.   *C. gigas* 11.

  b. Sheaths golden, with both inner and outer layers hyaline and colorless.   *C. Baileyi* 12.

1. Calothrix Braunii Bornet & Thuret

Ann. Sci. Nat. Bot., 8, 3, p. 368, 1886.

Stratum velvety, blue-green to brownish. Filaments straight, parallel, often crowded, swollen and often bent at the bases, 9–10μ in diameter and up to 500μ in length. Sheaths thin, close, colorless, homogeneous. Trichomes 6–7μ in diameter, often but not always constricted at the cross walls, tapering into long hairs; cells a little shorter than their diameter. Heterocysts basal, hemispherical. Resting cells absent.

Cosmopolitan and common in standing or flowing water on stones, shells, and water plants, it has been reported from several localities in the United States. There have been no records for it from the Yellowstone. It is quite common in cool standing or flowing water throughout the Park, growing on stones, etc. It has been noted in Panther Creek (Gallatin Mountains), Yellowstone River, Gibbon River, Yellowstone Lake, and in several smaller bodies of water. In the Yellowstone Lake at West Thumb, it grew in water slightly warmed by nearby hot springs. The species is evidently non-thermal.

2. Calothrix Geitleri, sp. nov.

Filaments single or in tangled clumps in and on the strata of gelatinous algae. Filaments up to 800μ in length, flexuous and usually entangled and contorted, slightly swollen at bases, and tapering gradually into long colorless hairs, diameter of filaments at base up to 9μ, five cells from base 6–8.5μ, hair cir. 1.5μ. Trichomes often constricted at cross walls in basal part, otherwise
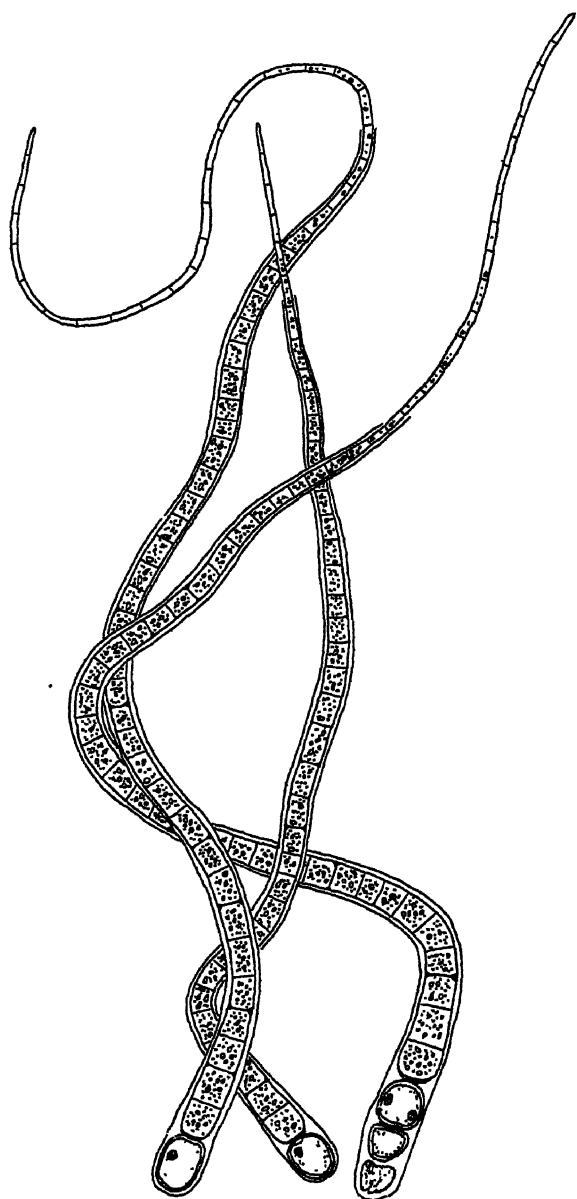
FIG. 47.—*Calothrix Geitleri* (×640).

rarely constricted. Cells usually longer than their diameter, from 0.8–2.0 diameters in length, in hairs up to 4 diameters; cells 5–6μ in diameter at base, 4–5μ five cells from base, 1.5μ in hairs; cell contents blue-green, each cell with several granules of variable size. Sheaths close, cir. 1μ thick, colorless, homogeneous, somewhat gelatinous. Heterocysts basal, as large as or larger than the trichome bases, within the sheath, usually single, sometimes 2–3 present, mostly ellipsoidal, 6–7μ in diameter by 5–9μ in length; when more than one is present, the terminal one is usually obtusely conical. Hormogonia long, infrequent. Resting cells absent.

While close to several other species, this plant resembles especially *C. Weberi* Schmidle, *C. javanica* De Wild. and *C. Braunii* Born. & Flah. From *C. Weberi* it may be separated by its more slender filaments, its gradually tapering form, and usually unconstricted trichomes. It differs from *C. javanica* in having a more easily observable sheath, more swollen base, by lack of resting cells and by heterocysts larger than the trichome bases. The chief points of departure from *C. Braunii* are its solitary or tufted habit of growth, more slender filaments, longer cells, and larger heterocysts (*C. Braunii* may have trichomes with obscure constrictions).

I have named the species in honor of Dr. Lothar Geitler, of Vienna, Austria, whose works on the Blaualgen have been of great help to all students of the group.

C. Geitleri has been found only at West Thumb imbedded in the strata of *Phormidium laminosum* (Ag.) Gom., at 37° C.; the spring in which it grew is yet unnamed. The type (no. 448) collection contained scattered tufts and single filaments shallowly imbedded in the *Phormidium* and mostly with the hairs emerging from it. The strata of *Phormidium* bearing the *Calothrix* was partly emersed, forming algal "islands."

3. Calothrix charicola, sp. nov.

Filaments solitary or in small clumps, without order, unbranched, epiphytic on *Chara*, attached by prostrate basal portion and with free tips, mostly about 500μ long (up to 700μ), including the 300–400μ long colorless apical hair; straight or flexuous, often slightly and abruptly bent just above attached and prostrate basal portion; bases of filaments feebly swollen, 10–12μ in diameter, middle portions 6–8μ in diameter, and gradually tapering into the long colorless hairs 2μ in diameter near apices. Trichomes 5–7μ in diameter at base and gradually tapering. Sheaths firm near bases, of moderate thickness, 1.5–2.0μ thick, golden brown, homogeneous, gradually becoming thinner and colorless toward bases of hairs, colorless, gelatinous, and frayed out at bases of hairs. Cells, at base, 1/3–2/3 diameter in length, toward apices gradually becoming longer, and 3–4 diameters in hairs, usually constricted at cross walls in basal parts, not constricted above; cell contents homogeneous, bright blue-green. Heterocysts basal, single, mostly hemispherical, less often spheroidal, at first
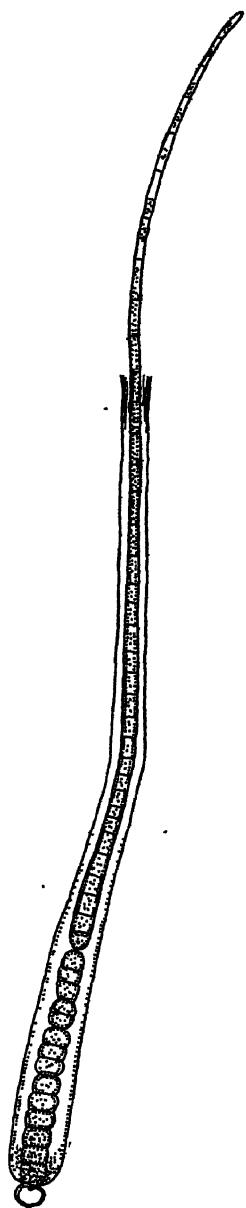
FIG. 48.—*Calothrix chari-
cola*, short but typical
filament (×635).

inclosed by the sheath, later exposed, 5–7µ in diameter. Resting cells absent.
Hormogonia frequent. produced few at a time near bases of filaments.

The species is sufficiently distinct from other species to be easily recog-
nized. Comparatively few species of *Calothrix* have been found as
epiphytes on larger algae in thermal situations.

Growing on sterile plants of *Chara* in Soda Spring, Mammoth Hot
Springs, at 27–30° C., pH. 6.5 (type: no. 128, 29.5° C., pH. 6.5), in
quiet water. *C. charicola* is very local in distribution. This is possibly to
be correlated with the rather rare occurrence of springs of the type of the
one in which it was found. The high salt content, slightly acid reaction,
and stagnant tepid water are unusual among the Yellowstone springs.

4. CALOTHRIX FUSCA Born. & Flash.

Rev. des Nost., p. 364, 1886.

Filaments in the matrix of gelatinous algae, single or in small and indefinite
tufts, rarely abundant enough to almost cover the substratum, straight, flex-
uous or contorted, unbranched or sparingly branched, with swollen bases and
tapering into moderately short thin hairs; diameter at base up to 17µ, body of
filaments 10–12µ, hairs as small as 1.7µ, length 200–300µ. Sheaths colorless,
soft, lamellate but often indistinctly so, up to 2.7µ in thickness. Trichomes
tapering uniformly from base to apex, not constricted at cross walls. Cells
shorter than their diameter, often disk-shaped, becoming longer in the hairs,
up to 12µ in diameter at base, 7–8µ in middle of filaments, and gradually be-
coming more slender; cell contents blue-green to olive-green, frequently with a
few conspicuous granules. Heterocysts basal, single (or infrequently in pairs),
hemispherical and usually slightly concave on face toward trichome bases;
smaller in diameter than the basal trichome cells. Resting cells absent.

I was able to confirm the occasional occurrence of two heterocysts at
the trichome base. The branching was strikingly rare in the Yellowstone
material, being observed in only two filaments.

C. fusca is a common and cosmopolitan alga growing in *Nostoc, Gloeo-
trichia, Batrachospermum, Chaetophora, Tetraspora, Gloeocystis, Riv-
ularia,* etc. Its known range includes all the continents except Australia
and Antarctica. It had not been reported from the Yellowstone.

In the Park it probably occurs most frequently on *Nostoc* species [esp.
N. verrucosum (L.) Vauch. and *N. pruniforme* (L.) Ag.]. It is most
frequently non-thermal. In the Firehole River at the Biscuit Basin and
at Geyser Hill (Upper Geyser Basin), where the water shows strongly
the effects of the entrance of thermal waters (hot spring and geyser
overflows), it is quite abundant on *Nostoc verrucosum* and on *Rivularia
globiceps,* forming on some colonies an almost solid stratum. The most

abundant site was in the Biscuit Basin just below the entrance of Black Pearl Spring overflow (no. 433, 22.5° C., pH. 8.2). At this place it was accompanied by well-marked thermal species of the cooler range. The highest temperature at which it was found was 25.7° C., within a few feet of the above-mentioned point. In strictly non-thermal waters of the Park I have found the species in the Firehole Cascades, Gibbon River one half mile above the falls, Yellowstone River at Hayden Valley, Panther Creek three miles west of the Seven-mile Bridge over the Gardiner River, all on *Nostoc* species; in the Gardiner River at the Seven-mile Bridge, on *Tetraspora;* in the Yellowstone River at Fishing Bridge, on *Chaetophora;* and in the Firehole River at junction with Madison River, on *Gloeotrichia.*

5. CALOTHRIX PARIETINA Thuret

Essai class. Nostoch., p. 381, 1875.

Filaments single, in tufts, or in spreading crustaceous brown to almost black strata, often incrusted with lime or silica, usually unbranched, branching rare, erect, decumbent or irregular, flexuously contorted or more or less flexuous, 10–12μ (or rarely up to 18μ) in diameter, and up to 1 mm. long. Sheaths close, moderately thick (1–2.5μ), lamellate, brown and more or less ochreate, often opaque, fragile and often fissured, wide and often fringed in upper portions. Trichomes 5–10μ in diameter, bearing a long colorless hair, usually constricted at cross walls below, cylindrical above. Cells short in basal parts, 0.3–0.7 diameter in length, longer in upper portions, up to 2–3 diameters, blue-green, with usually several granules in each. Heterocysts basal, single or in pairs, occasionally intercalary; basal heterocysts subspherical to button shaped, usually hemispherical, larger than the trichome bases; when two are present, the subterminal one is usually quite flattened; intercalary heterocysts elliptical to subcylindrical. Hormogonia about 3 times as long as broad, single or in series of a few. Resting cells absent.

Widely distributed and cosmopolitan, it grows in a wide range of habitats: ponds and lakes, often in the littoral zone on stones and pebbles, moist earth, rocks, and cliffs, brackish water, and damp soil in salt marshes. It has been reported from several localities in the United States, although not from the Yellowstone.

The species is quite frequent in the Park on wet rock and in some shallow pools. At West Thumb it has been noted on wet sinter rock, at the edge of Yellowstone Lake. This locality is interesting in that the alga was on rock kept wet by seepage from hot springs nearby. The range of temperature here was 18-23° C. (no. 449). In Bijou Geyser, Upper Geyser Basin, it was found at a much higher temperature, 37° C. (no. 438). It seems evident that this non-thermal species is encroaching on thermal habitats to a significant degree.

6. CALOTHRIX THERMALIS (Schwabe) Hansgirg

Beiträge zur Kenntniss der Böhmisch. Thermalalgenflora, Osterr.
Bot. Zeitschr. 34, p. 279, 1884.

Syn.: *Mastichonema thermale* Schwabe, 1837.

Stratum tomentose, often slippery, often lime-incrusted, extended, blue-green, olive-green to dull or bright yellow-brown. Filaments interwoven, contorted, thickly placed, 8–10μ in diameter by up to several mm. long, feebly swollen at bases of at least young filaments. Sheaths moderately thick, colorless or usually at bases of older filaments yellowish, or mostly yellowish, mostly indistinctly lamellate, sometimes almost homogeneous, sometimes distinctly lamellate. Trichomes tapering into long hairs, feebly or not constricted at cross walls. Cells 5–8μ in diameter, 1/3–1 diameter in length (rarely longer ?), blue-green. Heterocysts basal and often intercalary, elliptical to subspherical. Resting cells absent.

This cosmopolitan thermal alga has been reported from the United States only by Weed (1889) and Tilden (1898). Their records are subject to doubt or amendment. Weed refers to the alga as growing in the runoffs of the geysers. It is rare or absent in such sites. He neither distinguished between the various species of *Calothrix,* nor separated *C. thermalis* from *Dichothrix.* Apparently to both Weed and Tilden a thermal *Calothrix* was of necessity *Calothrix thermalis.* Tilden cited records of her own for *C. thermalis* in the Yellowstone, and published five figures of the plant (Tilden, 1910, pl. 18, f. 1-5). Her Fig. 3 is not *C. thermalis;* figs. 4 and 5 probably are not; figs. 1 and 2 probably are the species.

C. thermalis is abundant in the Yellowstone, especially at the Mammoth Hot Springs. It has been noted in Orange Spring Mound, Orange Spring Mound, Jr. (nos. 83, 84, 85) at 25-42° C., pH. 7.95-8.2, as a dominant form, Angel Terrace, Hymen Terrace, Jupiter Terrace, Diana Terrace, Main Terrace, White Elephant Spring, and elsewhere. In other parts of the Park it has been found occasionally. It was noted at the Lower Geyser Basin: White Dome Geyser, pool by cone (nos. 404, 405) at 19.2-20° C., pH. 8.4; and in the Twin Buttes Region: Spray Geyser (no. 427) at 39.3° C., pH. 9.0. The plant is one of the most characteristic species in the Mammoth Hot Springs at temperatures of 20° C. to 50° C., and between 30° C. and 40° C. it is regularly a dominant form. It has been found only in basic waters, pH. 7.4-9.0. The species is regularly thermal, and has not been noted in the Park outside of thermal waters.

7. Calothrix coriacea, sp. nov.

Stratum extended, leathery, brownish black, 1–2 mm. thick. Filaments very long, up to 5 mm. in length, contorted and interwoven, 10–15μ in diameter, tapering very gradually in the upper half into a short hair or a pointed filament apex, not swollen at bases, branching rare or absent. Sheaths lamellate with parallel lamellae, yellowish in basal half of filament, colorless in upper half, firm, even, smooth. Trichomes cylindrical, not constricted at cross walls, 3–7μ in diameter, up to 6μ in diameter at base. Cells elongate, 1.5–6.0 diameters in length, with blue-green, granular contents. Heterocysts basal and intercalary; basal heterocysts 1–2, ovoid with flattened face to spheroidal or hemispherical, 6–8μ in diameter by 4–12μ in length; intercalary heterocysts single, cylindrical, 4–7μ in diameter by 8–27μ in length. Hormogonia 10–30-celled, constricted at the cross walls, with short cells (0.5–1.0 diameter in length). Resting cells absent.

Differing from related species by mostly minute but numerous features, *C. coriacea* is distinct. From the associated Yellowstone species it is easily separated by its thin, dark, tough, leathery stratum.

It has been found only in the Upper Geyser Basin. The type (no. 436) is from Bijou Geyser, where it grew on a mixed stratum of *Phormidium subcapitatum* Boye Pet. and *Phormidium rubrum* Tilden, at 42° C., pH. 8.95. Its stratum entirely covered the stratum of *Phormidium* and appeared to injure it severely. It has been noted around several geysers in the immediate vicinity of Bijou: Mastiff and Catfish Geysers, Oblong Geyser overflow, Lion Geyser overflow, and others at temperatures of from 35° to 49.6° C., in basic waters. It grows either emersed or submerged, on rocks or on other algae.

8. CALOTHRIX KUNTZEI Richter

in Kuntze, Revisio Gen. Pl., 3,2, p. 388, 1898.

Stratum extended, pilose, carpet-like, up to 5 mm. in thickness; above dull blue-green to golden brown, becoming paler toward the lower portions, incrusted with silica below. Filaments in tufts, mostly erect and mostly parallel, straight to flexuous or in lower portions frequently contorted, 10–13μ in diameter, occasionally with single false branching; filaments often sheathed with a siliceous incrustation. Trichomes often swollen at bases, 5–8μ in diameter in middle portions and up to 10μ at base. Cells blue-green, cylindrical to slightly swollen, shorter or longer than broad. Trichomes very long, up to 3 mm. or more, tapering at apices into long colorless hairs with elongate cells, usually constricted at the cross walls. Sheaths firm, thick, colorless or usually golden, lamellate, made up of divergent trumpet-shaped segments, and with occasional flaring free collars. Resting cells absent. Heterocysts both basal and spherical, and intercalary and quadrate to cylindrical, up to 7 diameters in length, and often in catenate series.
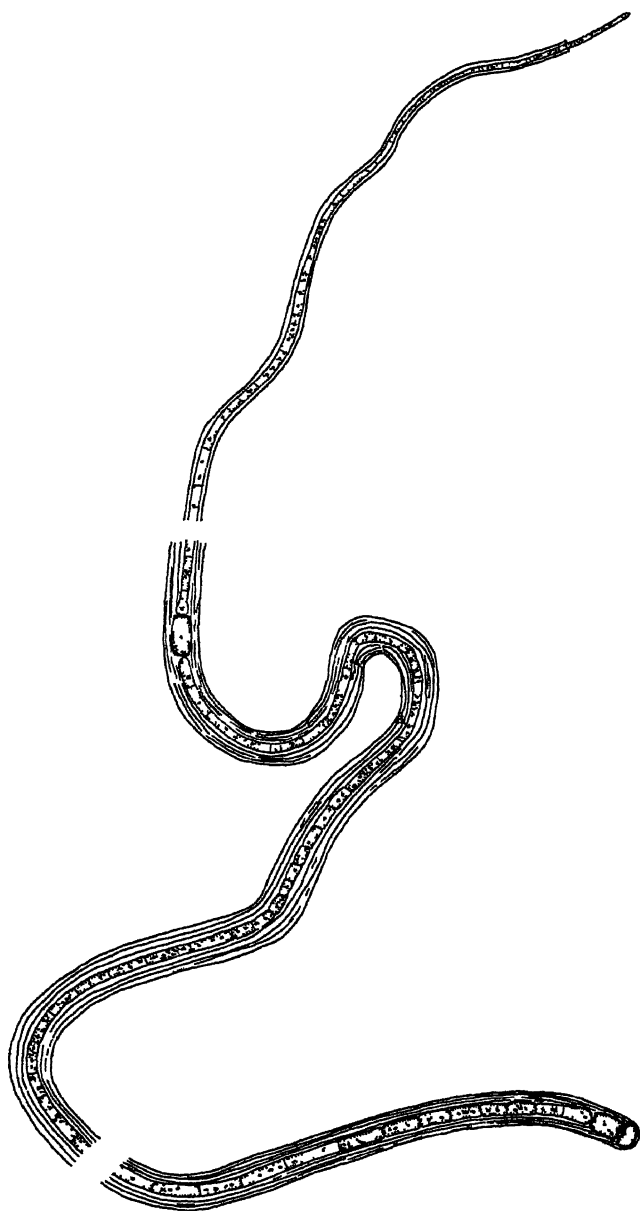
FIG. 49.—*Calothrix coriacea* (×345).

This species is close to *C. calida* Richter in many respects. Geitler (1931) suggested that the two might be identical. This view is especially favored by Richter's rather brief descriptions, that scarcely note the more striking differences. For example, Richter noted the elongate intercalary heterocysts of *C. Kuntzei* but merely mentioned the presence of intercalary heterocysts in *C. calida* without any reference to their shape or size; he noted the thickness of the strata: 5 and 6 mm., poor grounds for their separation; and gave similar dimensions. The two species, while close, are certainly distinct. The rather more pilose strata, the much elongate intercalary heterocysts, the catenate heterocysts are all in sharp contrast to *C. calida*. The description given above is scarcely that of Richter.

C. Kuntzei is a typical member of the flora of certain eruptive geysers. It is found on the sinter slope of most of the major geysers in the Upper Geyser Basin and a few of those in the Lower Basin; it occurs around several non-eruptive springs. Richter described the species from material collected by Kuntze in "Yellowstone Geysers," in Oct. 1874. Although Kuntze did not state exactly where he collected the material, it probably came from the Upper Basin. Since that time until now, to my knowledge, the species has not been reported.

I have found the plant at the following springs:—Upper Geyser Basin: Giant Geyser, Bijou Geyser (nos. Y. 27, 135, at 44.5° C., pH. 8.95), Castle Geyser (no. OS. 47, at 30-55° C., pH. 9.1), Old Faithful Geyser, Lion Geyser, Grand Geyser, Dragon Geyser, Beehive Geyser, and Grotto Geyser; Midway Geyser Basin: Grand Prismatic Spring, and Excelsior Geyser Crater; Lower Geyser Basin: Great Fountain Geyser, White Dome Geyser, and Fountain Geyser. The plant is very resistant toward desiccation, which is particularly severe on the intermittent and eruptive springs. On the other hand, it is often killed by the hot water when the water falls a little farther than usual from the vent, or when the eruption is greater than usual. Giant Geyser and Lion Geyser each scalded out an extensive patch of the alga in the summer of 1931. Giant Geyser is sufficiently intermittent to permit the alga to grow up between eruptions, so that the water merely killed out the advance made during the period of quiescence; Lion Geyser killed out the growth by overflowing rather than erupting, thus heating its slopes more than it does with a normal eruption. *C. Kuntzei* seems to be limited to basic waters (pH. 8.4-9.3) and to tolerate a wide temperature range (25-55° C.).

9. CALOTHRIX CALIDA Richter

in Kuntze, Revisio Gen. Pl. 3,2, p. 388, 1898.

Stratum extended, somewhat pilose, carpet-like, up to 6 mm. in thickness, spongy or crustaceous, olivaceous to dull brownish, frequently incrusted with silica or lime below. Filaments interwoven, flexuous to contorted, not in tufts, 8–10μ in diameter and up to 5 mm. in length, with occasional single false branching. Sheaths close, firm, thick, yellowish-brown except near bases of hairs, lamellate with gradually divergent lamellae, at infrequent intervals with flaring, funnel-shaped collars. Trichomes feebly swollen at bases, 3–6μ in diameter, up to 7μ in diameter at base, blue-green, tapering into long hairs with elongate cells, constricted at the cross walls. Cells below mostly swollen, 1–3 diameters in length, longer than broad, quadrate to short-cylindrical, above cylindrical, 2–3 diameters in length, and often with inconspicuous cross walls. Heterocysts basal and spherical to subspherical, intercalary and spherical, ovoid or short-cylindrical, 1.0–1.8 diameters in length, single. Resting cells absent. Hormogonia present.

Reported by Richter from geysers in Yellowstone, at 62.5° C., *C. calida* is apparently an endemic species. Richter's temperature record is probably erroneous, due to the periodic fluctuation in the activity of the associated geyser.

C. calida is much less abundant than the similar *C. Kuntzei,* and is apparently more widely distributed. It has been noted in the Upper Geyser Basin: Giant Geyser, Old Faithful Geyser, Lion Geyser, and in a few other springs; Mammoth Hot Springs: Minerva Terrace (no Y. 12), Jupiter Terrace; and in five isolated springs. It occurred at from 29° C. to 40.4° C., pH. 8.0 to 8.85. In a few sites it was abundant and formed unmixed strata.

10. Calothrix cavernarum, sp. nov.

Stratum firm, pilose, carpet-like, vertically fibrous, up to 5 mm. in thickness, brown on surface and in upper portions, paler below, frequently incrusted with silica, especially below. Filaments in part erect and mostly parallel, in part suberect and flexuously contorted, swollen at bases especially when young, 14–20μ in diameter above the base, up to 24μ in diameter at the base, tapering into short colorless hairs. Trichomes 5–9μ in diameter and up to 3 mm. or more in length; constricted at the cross walls in the basal portions, and at intercalary meristems above, otherwise cylindrical and unconstricted. Sheaths close-fitting, wide, golden brown to yellowish except near bases of hairs where they become colorless, distinctly lamellate, lamellae parallel and not divergent, rather brittle and often cracked in older filaments, flaring and funnel-shaped at the upper end, incrusted with silica and frequently peeling in basal portions. Cells 0.7–3.0 diameters in length, short at base and in meristems, elsewhere 1.5–3.0 diameters (including the apical hairs); contents blue-green, occasionally with granules; cross walls inconspicuous. Heterocysts basal, one to three together, and intercalary, single or in twos; basal heterocysts spherical to sub-
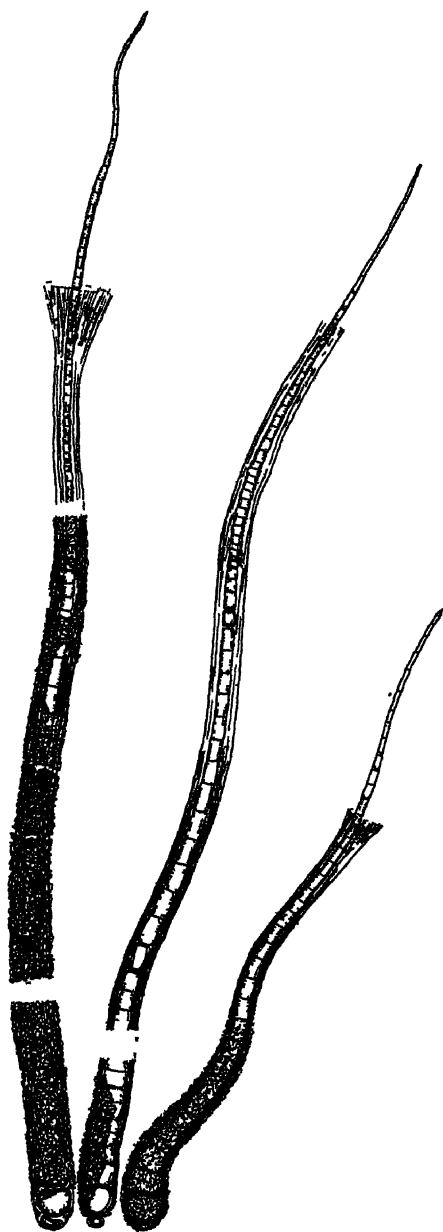
Fig. 50.—*Calothrix cavernarum*, filaments
incrusted with silica (×265).

spherical, 9.0–12.5μ in diameter by 10.0–12.5μ in length, when two are present the terminal one smaller and often flattened, 6–7μ in diameter by 3–8μ in length; intercalary heterocysts cylindrical, 6–9μ in diameter by 7–30μ in length. Branching rare. Hormogonia not frequent, long. Resting cells absent.

C. cavernarum is distinct. It is closer to *C. Kuntzei* than to the other Yellowstone species. From it it differs in its larger size, frequent multiple basal heterocysts, infrequent branching, and other minor details.

The species is rare and local. It has been found in a single site, but there in great abundance over an area of some five square feet. It was growing in a cave formed by an overhanging ledge of sinter, on the bank of the Firehole River between Oblong and Giant Geysers, Upper Geyser Basin. The plant was in moderate shade and at 25° C., on wet sinter (type: no. 446).

11. Calothrix gigas, sp. nov.

Stratum extended, gelatinous-fibrous to woolly-gelatinous, bluish-green, less often brownish-black, up to 3 mm. in thickness. Filaments entangled below, ascending and more or less parallel above, flexuous to straight, tapering abruptly or somewhat gradually into short hairs, feebly swollen at bases, 18–32μ in diameter, mostly cir. 20–25μ, slightly thicker at bases in young filaments than in middle portions. Sheaths thick, lamellate with divergent lamellae, golden-brown with a colorless, homogeneous and gelatinous surface layer 0.5–2.5μ thick; sheaths pigmented to the open, flaring ends at bases of hairs, pigmented even in young filaments, branching single, occasional. Trichomes up to 10μ in diameter at bases, 4–6μ in diameter in middle portions, and 1.5–2.5μ in hairs, mostly not constricted at cross walls, constricted in meristematic regions and at bases. Cells often slightly swollen, cylindrical, 1.5–2.5 diameters in length, as short as 0.5 diameter in meristems, cross walls often inconspicuous: cell contents coarsely granular, blue-green. Heterocysts basal and intercalary, basal heterocysts spheroidal to hemispherical, 6–11μ in diameter, intercalary heterocysts cylindrical, 1.5–4.0 diameters in length, 14–28μ long, by 6–12μ in diameter. Hormogonia present. Resting cells absent.

The young plants are often prostrate and tapering at both ends, and have the general aspect of *Scytonematopsis*. I am terming this juvenile stage the Scytonematopsis state. The filament size and sheath characters are constant in both the adult and juvenile states. The species is quite distinct.

It has been found in the Upper and Lower Geyser Basins and in the Twin Buttes Region. The type (no. 430) is from the junction of Spray Geyser overflow and Imperial Geyser creek, where it grew at 31.5° C., pH. 9.05, on wet sinter at the edge of the stream. On the whole it is not common. It was noted (no. 426), in its Scytonematopsis state, on wet sinter by the Spray Geyser rill at 32.4° C., pH. 8.9. In the Lower Geyser
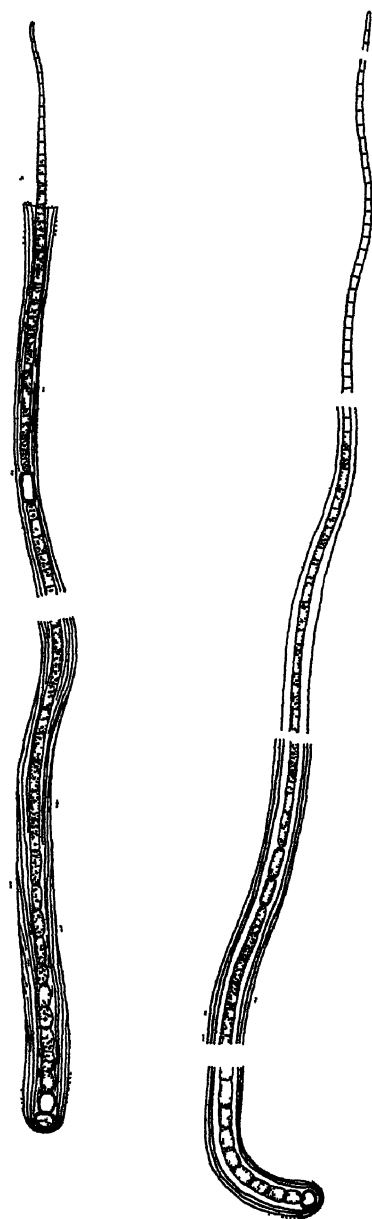
FIGS. 51, 52 —Left, *Calothrix gigas*
(×275); right, *Calothrix Baileyi*
(×265).

Basin it was found at the Great Fountain Geyser, in the Upper Basin at a seep on Geyser Hill.

12. Calothrix Baileyi, sp. nov.

Stratum firm, pilose, carpet-like, vertically fibrous, covered with a finely fibrous whitish down consisting of the free hairs at ends of trichomes, extended and 10 mm. or more in thickness, very smooth and slimy on surface, dark orange-brown to brown, grayish below; surface layers to 3 mm. almost free from incrustation, deeper layers heavily incrusted with lime. Filaments rarely branched, very long, in fascicles, parallel, erect, 16–23μ in diameter, feebly swollen at bases, tapering into long free hairs. Sheaths firm, thick, hyaline at first, becoming golden-yellow to golden-brown, with a colorless outer layer and a colorless inner layer, lamellate with parallel layers, often breaking at or near points of active growth, the colorless portions stretching and forming colorless, often constricted, transverse zones in the sheaths, no fraying or divergence at points of breaking. Trichomes 5.0–7.2μ in diameter, swollen at bases only when young, tapering into colorless hairs up to 4 mm. in length. Cells 2–4 diameters in length, cylindrical to subcylindrical. Cross walls often not conspicuous; filaments usually not constricted strongly at cross walls, often slightly or not at all constricted; cells often swollen; contents blue-green, granular. Heterocysts basal and intercalary, basal ones solitary and hemispherical, intercalary ones cylindrical, cir. 5 diameters in length, 5–8μ in diameter, solitary or in pairs with or without a cell between. Resting cells absent. Hormogonia not noted.

The species is completely distinct but related to *C. Kuntzei* Richter, *C. calida* Richter, *C. cavernarum* (of this paper) and *C. gigas* (of this paper). Its sheaths are distinctive and its massive stratum unique.

C. Baileyi has been named in honor of Mr. Kenneth Bailey, of Richmond, Ind., who gave the author invaluable assistance in the Yellowstone in the summer of 1931 and who discovered the plant.

Although found only on the banks of the Boiling River in the Gardiner River Canyon, the strata of the plant cover large areas of wet hot earth and rock. The plant grew on both banks of the Boiling River for its entire length, and was especially well developed where it received the spray from a small waterfall. It grew at temperatures of 32–48° C., and at pH. 6.6. The type (no. 261) was at 35.2° C.

GLOEOTRICHIA Agardh

Alg. Maris Medit. et Adriat., p. 8, 1842.

Filaments radially arranged and more or less parallel, united into spherical or hemispherical colonies, frequently but often obscurely false-branched, tapering into long, colorless hairs; branches single. Sheaths mostly close; firm and distinct at bases and only the outer part gelatinized, completely or almost

completely gelatinized and confluent above the bases, and often indistinct; gelatinized sheaths forming a general colonial matrix. Trichomes with intercalary or trichothallic growth, tapering. Heterocysts basal and often also intercalary, usually present at bases of branches. Resting cells at the bases of trichomes near the basal heterocysts, single or in series of a few. Hormogonia present. Pseudovacuoles in certain species.

Many authors have united this genus with *Rivularia* Ag. The two are unquestionably close, but ordinarily the presence or absence of resting cells makes their separation easy.

The majority of the species grow in fresh water, attached at first and later floating free. Planktonic, brackish, and terrestrial forms are few. There are no thermal species.

In the Yellowstone the genus is relatively unimportant, and is best represented in some of the smaller rivers.

KEY TO THE YELLOWSTONE SPECIES

I. Colonies hollow at maturity; sheaths yellowish; cells usually without pseudovacuoles.   *G. natans* 1.
II. Colonies solid; sheaths colorless; cells with pseudovacuoles.
                                                           G. echinulata 2.

1. GLOEOTRICHIA NATANS Rabenhorst

Deutschl. Krypt.-Fl., p. 90, 1847.

Colonies spherical to subspherical, soft, solid when young and hollow at maturity, mostly up to 1–3 cm. in diameter, sometimes larger, rarely much larger, dull olive-green to brown. Filaments loosely associated, easily separated from each other with light pressure. Trichomes tapering into long hairs at apices. Sheaths yellowish to golden, narrow, and in the basal part inflated and constricted in a few places. Cells 5–7μ in diameter, olive-green to blue-green, in basal parts swollen, quadrate or shorter than long, above cylindrical, up to 4 diameters in length; intercalary meristems with shorter and swollen cells; cell contents granular, in young colonies sometimes with pseudovacuoles. Heterocysts spherical or subspherical, 6–12μ in diameter. Resting cells single, cylindrical, straight or curved to crooked, 10–18μ in diameter by 40–250μ in length, with colorless to brownish smooth membranes.

Occurring in standing or slowly flowing, fresh or rarely feebly brackish water, *G. natans* is cosmopolitan and locally very abundant. Its occurrence is often erratic on successive seasons in the same site. It has not been previously reported from the Yellowstone.

It has been collected a single time in the Firehole River at the Biscuit Basin (no. 432), at 22.5° C., pH. 8.2. The colonies were mostly attached, some were floating. The water where the attached plants were found was warmed by the overflows of springs in the Biscuit Basin and

Upper Geyser Basin above. The plant is non-thermal, and shows little ability to invade warm waters. It was noted but not collected in non-thermal waters elsewhere in the Park.

2. GLOEOTRICHIA ECHINULATA (Smith) Richter

Forsch.-Ber. Plön 2, p. 31, 1894.

Colonies livid green to milky green, planktonic, solid, firm, spherical to ovoid; 0.5–7.0 mm. in diameter. Filaments easily separated from each other with light pressure. Sheaths thin, homogeneous, more or less easily visible, colorless. Trichomes tapering into long hairs which project free from the gelatinous matrix of the colony, at base 8–10μ in diameter, in hairs 1–2μ. Cells at base quadrate and swollen, often spheroidal, above longer and cylindrical, with pseudovacuoles. Heterocysts ellipsoidal to spherical, 7–10μ in diameter. Resting cells cylindrical, straight or feebly bent, 8–18μ in diameter by cir. 44–50μ in length.

This planktonic species is known from North America and Europe. It is most frequent in standing water, ponds, and lakes; it is occasional in flowing water. It has not been noted previously in the Yellowstone.

It has been found in abundance in the Firehole River opposite the Biscuit Basin (nos. 431, 433) at 22.5° C., pH. 8.2, in slowly flowing water warmed slightly by hot spring overflows. The colonies were mostly cir. 2-3 mm. in diameter and were floating among water plants. A single colony was found at the junction of the Gibbon and Firehole rivers, several miles below the Biscuit Basin. The plant was looked for but not found elsewhere. It seemed to be absent above the Biscuit Basin.

RIVULARIA Agardh

Syst. Alg., p. 19, 1824.

Filaments more or less radial or parallel, united into spherical or hemispherical colonies; colonies often confluent into extended strata. Colonies gelatinous, cartilaginous, or (when indurated) stony. Trichomes with single false branching mostly distinct but sometimes obscured, tapering into hairs, with trichothallic or intercalary meristems. Sheaths mostly gelatinized and somewhat confluent in the outer portions. Heterocysts basal and often also intercalary, usually at bases of the false branches. Resting cells absent. Hormogonia formed mostly at the intercalary meristems.

The various species grow either in fresh flowing or standing water, on moist earth, rocks, etc., in salt marshes or marine habitats and mostly intertidal. Planktonic species are few. Several species are epiphytic on aquatic plants. Thermal species are unknown.

In the Yellowstone hot springs the genus is poorly represented and unimportant.

A single Yellowstone species.

1. RIVULARIA GLOBICEPS G. S. West

Linn. Soc. Bot. 38, p. 182, 1907.

Colonies soft, spherical to hemispherical, 1.5–3.0 mm. in diameter. Filaments easily separated from each other by light pressure. Sheaths thick, homogeneous, colorless, and difficultly visible. Trichomes tapering into moderately long hairs. Cells cylindrical, constricted at the cross walls, 4.8–6μ in diameter, 1.5–4.0 diameters in length in the basal parts, 1–3 diameters in length above, longer in hairs, blue-green in color; cell contents with a few conspicuous granules. Heterocysts spherical, single or rarely in pairs, 10–12μ in diameter.

Previously known only from Lake Tanganyika, Africa, growing on the stems of water-plants, the presence of this species in the Yellowstone is surprising.

It has been found two times in the Firehole River opposite the Biscuit Basin (nos. OS.42, 431, 432, 433). It was growing on various water plants for the most part, a few colonies were floating. The colonies were mostly spherical and the plants were typical in every respect. The water in which it grew ranged from 18.0 to 26.4° C., with a pH. of 8.2. This temperature was due to the warming effect of the overflows from hot springs in the Upper Geyser Basin and the Biscuit Basin, and probably approximated the temperature of the tropical lake the plant was described from. The Firehole River is in part quite rapid, but at the point at which this as well as several other interesting algae were found the water on the cast side was quiet and supported a heavy growth of aquatics.

MICROCHAETACEAE Lemmermann

Krypt.-Fl. Mark Brandenberg, p. 3, 1910.

A single Yellowstone genus.

MICROCHAETE Thuret

Essai class. Nostoch., p. 378, 1875.

Trichomes single in distinct sheaths, usually tapering slightly toward the apex or less often of the same diameter throughout, with distinct base-apical differentiation, not tapering into apical hairs. Filaments mostly attached, single, in tufts, or turf-like strata, unbranched or sometimes with single false branching. Heterocysts basal and often also intercalary. Resting cells single or

less often in rows, adjacent to or near the basal heterocyst, rarely removed from it. Hormogonia present.

Type species: *Microchaete tenera* Thuret.

The several species live either in shallow water in the ocean, or in standing fresh water. Thermal species have not been noted previously.

A single rather uncommon species represents the genus and family in the Yellowstone thermal springs. There are few records of fresh water species from the United States and none from the Yellowstone.

A single Yellowstone species.*

1. Microchaete bulbosa, sp. nov.

Plants endophytic in the thallus of gelatinous algae, flexuous to contorted, in tufts or solitary; filaments unbranched or rarely with single false branching, up to 2 mm. in length but mostly less than 1 mm., swollen at base and tapering soon into an almost cylindrical and very gradually narrowing middle portion that ends in a blunt slender apex, diameter of filament at base 7–11μ, in middle part 5.3–6 0μ, at apex 3.8–4.2μ. Trichomes sharply swollen at bases of most filaments, mostly not constricted at cross walls except near the base, diameter at base 6.5–9.0μ, in middle part 4.2–5.0μ, at apex cir. 3μ. Sheaths firm, thin, colorless, homogeneous, often constricted opposite cross walls, giving the filament a moniliform appearance. Cell contents blue-green, mostly with 1–4 prominent granules, finely granular; cells cask-shaped to cylindrical, at base 0.7–1.5 diameters in length, in middle portion 1–3 diameters, at apex 2–4 diameters; end cells elongate conical with rounded apices, cir. 3.0μ in diameter by 7–9μ in length, wall of end cell slightly thickened. Heterocysts mostly basal and single, occasionally in twos, occasionally intercalary; basal heterocysts spherical to hemispherical, 5–10μ in diameter by 4–10μ in length; intercalary heterocysts barrel-shaped to cylindrical, 5–6μ in diameter by 10–13μ in length. Resting cells in rows of usually a great many, often all cells of a trichome becoming such, from 15 to 183 (probably often more), the row of resting cells often being separated from the basal heterocyst but not always; resting cells spherical to ovoid, 5–7μ in diameter by 5–12μ in length, shorter in basal part of trichome, longer in distal part, membrane smooth, thin, brown.

The long rows of resting cells separate *M. bulbosa* from most other species of *Microchaete*. Its closest ally seems to be *M. tenera* Thuret. From it it differs in having broader filaments, swollen bases, a more tapering form, larger heterocysts, shorter resting cells in longer rows, more prominent constrictions at the cross walls, and cells of the apical portions much shorter.

Up to the present the species has been found only in Spray Geyser Rill and Imperial Creek, Twin Buttes Region. There it inhabits the strata

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* *Tolypothrix distorta* var. *endophytica* might be sought here.

Fig 58 —*Microchaete bulbosa*, filaments of typical form, one with resting cells (×600)

chiefly of *Phormidium laminosum* (Ag.) Gom. at temperatures of 32–47° C., at an alkalinity of about pH. 9.0. The type (no. 427) is from the Spray Geyser Rill, at 39.3° C. and pH. 9.0. Apparently the species is not common in the Yellowstone but in the above locality it is easily found.

NOSTOCACEAE Kützing

Phyc. gen., p. 203, 1843.

NODULARIA Mertens

in Jürgens, Alg. Dec. 15, p. 4, 1822.

Filaments mostly straight or often bent; trichomes of short, disk-shaped cells, with thin, slimy or at maturity mostly confluent sheaths, single or united into formless slimy masses. Heterocysts intercalary, sometimes also terminal, slightly larger than the vegetative cells but similar in shape. Resting cells always removed from the heterocysts, single or in rows.

The species grow in fresh water, less often in brackish or salt water, and occasionally in warm springs. There are no previous records of the genus from the Yellowstone.

A single Yellowstone species.

NODULARIA HARVEYANA Thuret

Essai class. Nostoch., p. 378, 1875.

Filaments 4–6μ in diameter, more or less straight, with bluntly conical end-cells. Sheaths thin, colorless, distinct or confluent. Cells before division quadrate or nearly so, shorter following division. Heterocysts spherical with flattened ends. Resting cells in rows of 2–16, short cask-shaped to compressed-spherical, cir. 8μ in diameter, with yellowish brown membranes.

Growing in standing fresh or salt water, in salt marshes and in warm springs, it is widely distributed. In North America it has been found in many localities and in a variety of habitats.

In the Yellowstone it has been noted in seven stagnant or slowly flowing pools and streams. These include unnamed springs in the Upper and Lower Geyser Basins. In each site the water was basic, pH. 7.9–8.7, and was at most tepid, up at 32.8° C. The species is generally unimportant in the springs.

ANABAENA Bory

Dict. class. d'hist. nat. 1, p. 307, 1822.

Filaments solitary or united into indefinite slimy, flocculent or soft leathery strata or masses, straight, flexuous, contorted or coiled. Trichomes of the same diameter throughout, with delicate, soft and more or less confluent sheaths, often invisible, or none. Cells mostly at least as long as their diameters, constricted at the cross walls, ovoid to spherical, sometimes subcylindrical; all cells with normal pigmentation. Heterocysts intercalary. Resting cells solitary or in rows, spherical to cylindrical, either adjacent to the heterocysts, remote from them, or of indefinite position. Pseudovacuoles often present.

The majority of the many species are planktonic in fresh-water lakes and ponds, several species live attached or later often floating, a few regularly live on moist earth, etc., several occur in brackish water, a few in salt water, a few as symbionts in higher plants, and a few in warm waters. *A. oscillarioides* Bory, while ordinarily non-thermal, has been found several times in warm springs; *A. variabilis* Kütz. occurs on moist earth, in fresh water and in thermal situations; and *A. thermalis* Vouk was described from a hot spring in Croatia at 45° C. (Vouk, 1916). There are no previous records of thermal species for North America.

In the Yellowstone the genus is poorly represented and, in particular, planktonic species seem to be rare.

KEY TO THE YELLOWSTONE SPECIES.*

I. Resting cells ovoid, catenate; trichomes 4–6µ in diameter.   *A. variabilis* 1.
II. Resting cells cylindrical, solitary or in twos; trichomes cir. 1.3µ in diameter.
    A. Marklei 2.

1. ANABAENA VARIABILIS Kützing

Phycol. gener., p. 210, 1843.

Incl.: *Anabaena hallensis* (Jancz.) Born. & Flah.

Plant mass dark green, gelatinous, extended. Trichomes contorted and irregular; 4–6µ in diameter, mostly without sheaths but often imbedded in a soft gelatinous matrix. Cells barrel-shaped, lightly constricted at the cross walls, often with pseudovacuoles (?), 2.5–6.0µ in length, blue-green; end-cells obtusely conical. Heterocysts spherical or usually elliptical, cir. 6µ in diameter by 8µ in length. Resting cells ovoid, with truncate ends, 6–9µ in diameter by 8–14µ in length, not adjacent to the heterocysts, developing centrifugally in long catenate series, with smooth or minutely bristled, yellow-brown or colorless walls.

* *Mastigocladus laminosus* var. *anabaenoides* might be sought here.

Widely distributed and often common, it is found either on damp soil and mud or in water, floating or on the bottom, in fresh water, brackish, polluted, and warm waters. In the United States it is known from a large number of localities, ranging from Maine and New Jersey to California and Washington. In 1896 Tilden found *A. variabilis* in the Yellowstone on the surface of cool water in a ditch seven miles north of the Lake Hotel. There are no previous records of it from thermal sources, either in the Yellowstone or elsewhere in the United States.

In the present investigation it has been noted frequently in cool stagnant pools in the Geyser Basins, and but a single time (no. 443) in warm water. This collection was made in the Firehole River in the Upper Geyser Basin, where several hot springs empty into it. It was abundant at a temperature of 32.2°C., and at pH. 8.8. *A. variabilis* is clearly a species of non-thermal relationship that has invaded mild thermal situations to a limited extent.

2. Anabaena Marklei, sp. nov.

Filaments solitary or tufted, epiphytic on mosses in shallow water or on damp marshy ground, attached loosely and often becoming free floating, straight, slightly flexuous or sometimes irregularly crumpled, cir. 1.3μ in diameter. Cells cylindrical, cir. 1.3μ in diameter by 1.2-2.5 diameters in length, $1.5-3.0\mu$ long; slightly constricted at the cross walls; gray-green in color; end-cells rounded. Sheaths absent or at least invisible on free portions of filaments, poorly developed to easily visible on prostrate portions, thicker on the lower surface, colorless. Heterocysts few, barrel-shaped, cir. 2.5μ in diameter by 3.5μ in length. Resting cells mostly single, always removed from the heterocysts, cylindrical, $1.8-2.5\mu$ in diameter by $10-20\mu$ in length; membrane smooth, contents granular.
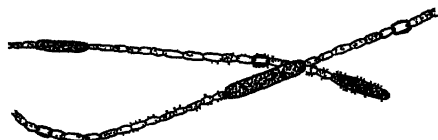
Fig. 54 —*Anabaena Marklei* (×770).

This extremely minute *Anabaena* can be separated from all other species of the genus by its size alone. It is of great interest as one of the smallest and most delicate of the heterocysted Myxophyceae. In its habit of growth it is reasonably distinct and does not seem close to any of the some forty members of the genus.

Anabaena Marklei has been named in honor of Dr. Millard S. Markle, Professor of Botany, Earlham College, Richmond, Indiana, who first interested the author in the Myxophyceae.

The plant has been collected regularly in the Norris Geyser Basin in the marshy siliceous "marl" flats of Tantalus Creek. The water supply of the flats is chiefly thermal and the water is warm and acid. Considerable areas are covered with a sparse growth of grasses and sedges, between which mosses grow in considerable profusion. On and among the moss plants the *Anabaena* is common. The only other alga noted in the formation was a species of *Microspora*. The temperature at which the *Anabaena* was found ranged from 38°C. to 22.7°C. The type (no. 109) was at 27.5°C. The acidity in the flat was quite constant, being throughout the area in which the plant was noted, pH. 4.9. There are no other stations for the plant.

<div align="center">

NOSTOC Vaucher

Hist. Conf. d'eau douce, p. 203, 1803.

</div>

Colonies of more or less definite form, gelatinous to cartilaginous, with or without firm outer colonial membrane, spherical, ovoid, bracket-shaped, disk-shaped, foliose, or rarely filiform, never tubular, but either hollow or solid, rarely confluent at maturity and indefinite. Trichomes uniform throughout, vegetative cells all alike. Sheaths often distinct, especially near periphery of colony, but mostly more or less confluent and often invisible, outer layers of sheaths confluent into a common colonial matrix. Filaments sometimes radially arranged in the inner part of the colony, usually without order, often interwoven, twisted, and contorted. Heterocysts intercalary or in the hormogonia terminal. Hormogonia produced from any part of the colony, mostly with terminal heterocysts, developing into the colonies by buckling and growth of the trichome, the sheath of the hormogonium becoming the membrane of the colony. Resting cells present in most species (all?), often in rows. Pseudovacuoles present in some species.

Many of the species of *Nostoc* are not distinctive and identification is apt to be somewhat inexact. Undoubtedly, numerous records are based on incorrect determinations. There are no previous records of the genus from Yellowstone Park. The numerous species occur in flowing or standing water, occasionally planktonic, on moist soil, rocks, etc.; a few are found in brackish water, a few symbiotic in higher plants; thermal records are few and strictly thermal species may be absent. *N. muscorum* Ag. has been reported from European hot springs, in particular by G. S. West from an Iceland geyser at 55° C. (!) The species is a well known non-thermal plant. Wood described *N. caldarium* from a hot spring at Owen's Valley, California, growing at 44-53°C. His

description is not diagnostic but it seems probable that he had *Mastigocladus laminosus* Cohn, or one of its varieties.

In the Yellowstone the genus is well represented in non-thermal sites and includes several abundant and important species. A few of these encroach to a varying degree upon available semi-thermal habitats. Apparently no true thermal species occur in the springs.

<div align="center">KEY TO THE YELLOWSTONE SPECIES.</div>

I. Colonies without firm outer membrane, more or less formless and soft; cells 2.5–3.0µ in diameter.   *N. cntophytum* 1.
II. Colonies with firm outer membrane; cells 3µ or greater in diameter.
  1. Surface of colonies smooth; cells 4µ or greater in diameter.
    A. Filaments not radially placed; colonies solid.
      a. Sheaths mostly distinct, yellowish, cells 5µ or more in diameter.
        *. Heterocysts 9–10µ in diameter; trichomes lightly to moderately constricted at cross walls.   *N. macrosporum* 2.
        **. Heterocysts cir. 7µ in diameter; trichomes deeply constricted at cross walls.   *N. microscopicum* 3.
      b. Sheaths indistinct, confluent; cells 4–5µ (mostly cir. 4µ) in diameter.   *N. sphaericum* 4.
    B. Filaments radially oriented; colonies hollow.   *N. parmelioides* 5.
  2. Surface of colonies roughened and warty; cells 3.0–3.5µ in diameter.
                                                                            N. verrucosum 6.

<div align="center">1. NOSTOC ENTOPHYTUM Bornet & Flahault</div>

<div align="center">Rév. Nostoch. hét. 4, p. 190, 1888.</div>

Colonies microscopically small, bluish-green to yellowish-brown, without firm outer membrane. Filaments closely packed. Sheaths narrow, at first colorless, later brownish, mostly distinct. Cells short barrel-shaped, 2.5–3.0µ in diameter. Heterocysts somewhat larger than the vegetative cells. Resting cells spherical or somewhat compressed, rarely longer than their diameters, 5–6µ in diameter by 5–8µ in length, with smooth, brown membranes.

Growing on water plants and in their dead empty cells, mostly in fresh but sometimes in brackish water, it has been previously known only from Europe.

In the Yellowstone it has been found a single time in considerable quantity on wet rock below a seep in Imperial Geyser Crater (no. 320), growing among other algae, at 41° C., and in slightly acid water. The associated algae were chiefly *Mastigocladus laminosus* var. *anabaenoides* Boye Pet., *Cylindrospermum stagnale* (Kütz.) B. et F., *C. marchitum* Lemm., and *Lyngbya subspiroides* (of this paper).

2. Nostoc macrosporum Menegh.

Monogr. Nost. ital., p. 116, 1843.

Colonies spherical, with firm outer membranes, solid, firm, mostly small, up to 1 mm. in diameter or rarely more, bluish to brownish green. Filaments at first closely packed, at maturity loose. Sheaths mostly distinct, yellowish, confluent in older colonies. Cells barrel-shaped, quadrate or disk-shaped, lightly to moderately constricted at the cross walls, 8–9μ in diameter, blue-green. Heterocysts almost spherical, 9–10μ in diameter. Resting cells rare, spherical or somewhat compressed, with thin, smooth membranes.

The species is very close to *N. microscopicum* Carm., and is possibly only a variety of it.

This cosmopolitan, terrestrial plant has been noted few times in the United States. It seems to be much more common than the records indicate. In the Yellowstone it is quite common in its normal habitats, moist earth, rocks, and cliffs. It is especially frequent on dripping rocks. It has not been found in thermal water but it does occur in places where thermal effects are visible. It was noted in the greatest abundance at Rustic Falls on Glen Creek (nos. 152, 153), at 15° C., pH. 8.5. In the West Thumb group of springs it was found on wet sinter at 22.7° C.

3. Nostoc microscopicum Carm. sec. Harvey

in Hooker, British Flora 5, p. 399, 1833.

Thallus spherical or elliptical, less often slightly irregular, usually quite small and microscopic, less often up to 1 cm. or rarely more in diameter, with a thick firm outer layer, olive-green to brown. Filaments at first somewhat densely entangled, in older colonies loosely so; sheaths mostly distinct, and yellowish to golden brown. Cells spheroidal, 5–8μ in diameter, pale blue-green to olive-green; deeply constricted at the cross walls. Heterocysts almost spherical, 7μ in diameter. Resting cells elliptical, 6–7μ in diameter by 9–15μ long, with smooth membranes, olive-colored.

This well-known and cosmopolitan species has been reported from numerous places in the United States, but has not previously been found in the Yellowstone. The plant occurs on moist earth, wet rock cliffs, among mosses in water or damp situations, and less typically submerged.

I have found the plant quite frequently in its usual habitats in the Yellowstone Park; wet rocks at the Gibbon Falls; seepy rock on Antler Peak, Gallatin Mountains; and on a damp shaded bank of the Gardiner River. A single collection (no. 449) was growing on a damp sinter cliff at the edge of Yellowstone Lake at West Thumb. At this place the temperature, 20° C., was greater than normal due to seepage of water from nearby thermal springs and, while not in itself warm, the water was of

thermal spring origin. It was growing mixed with *Phormidium foveo-larum* (Mont.) Gom. and *Calothrix parietina* Thuret.

4. Nostoc sphaericum Vaucher

Hist. Confer. d'eau douce, p. 223, 1803.

Colonies spherical or at length irregular, solid (very old colonies sometimes hollow by disintegration of central filaments) ; mostly 1–15 mm. in diameter but sometimes up to several cm.; olive-green, yellowish brown or violet-brown, with firm outer membrane. Filaments tangled, closely packed. Cells short barrel-shaped to almost spherical, 4–5μ (mostly 4μ) in diameter. Sheaths indistinct, confluent, often invisible. Heterocysts almost spherical, cir. 6μ in diameter. Resting cells elliptical, cir. 5μ in diameter by cir. 7μ in length, with smooth, brownish membranes.

Growing on moist earth, rocks, etc., in standing and slowly flowing water on water plants and rocks, and symbiotically with liverworts (*Pellia, Blasia, Anthoceros*), the plant is widely distributed and abundant. It is well known in North America, and has been found in Montana (Anderson and Kelsey) just north of the Yellowstone.

In the Park it is quite frequent in non-thermal sites and has been found as well in feebly warmed situations. In the Firehole River it occurred in water up to 29.8° C. The water in which it grew was neutral or feebly basic, pH. 6.7–8.45.

5. Nostoc parmelioides Kützing

Phycol. gen., p. 206, 1843.

Colonies attached firmly by a small area; disk-shaped, bracket-shaped, tongue-shaped, or rarely almost spherical, usually compressed but sometimes swollen, hollow, firm and leathery, with a firm smooth surface, up to 3 cm. in diameter. Filaments radiating from the center toward surface, somewhat straight and parallel toward center, twisted and entangled near surface. Sheaths mostly distinct and yellowish at the surface, mostly confluent and colorless within. Cells spheroidal to short barrel-shaped; 4–4.5μ in diameter by 0.5–1.0 diameter in length. Heterocysts spherical, cir. 6μ in diameter. Resting cells in rows, ovoid, 4–5μ in diameter by 7–8μ in length, with smooth, yellowish membranes.

This species is characteristic of rapidly flowing streams and is probably cosmopolitan. It has been found in North America, Europe, and Africa. It has been noted in localities with an elevation up to 11,000 feet. It is frequently found in very cold water in alpine streams. In the United States it is well known and widely distributed. Williams and Griffiths (1898) found it on rocks in the North Fork of Clear Creek, Big Horn

Mountains, Wyoming. It has not been previously reported from the Yellowstone.

In the Yellowstone it is one of the commonest non-thermal Myxophyceae and is present in abundance in almost all of the rapidly flowing permanent streams. It has been noted in the Yellowstone River, Firehole River, Madison River, Panther Creek (no. Y25), Gardiner River, and in several smaller streams. In the majority of sites it was in cold water. However, in the Firehole River opposite the Geyser Basins it occurred regularly at temperatures several degrees above normal. It was very abundant at 22.5° C. (no. 433, pH. 8.2), and was present in water as warm as 29.1° C. It was not found in any of the spring runoffs, but only in the river proper.

6. Nostoc verrucosum Vaucher

Hist. confer. d'eau douce, p. 225, 1803.

Colonies at first solid, spherical to hemispherical and smoothish, later becoming hollow, torn, often more or less confluent, with a wrinkled to warty surface, up to 10 cm. in diameter, olive-green, dark brown or greenish black, with firm outer membrane. Filaments in the periphery of the colony closely packed and contorted, within looser. Sheaths thick, distinct and yellow-brown at the surface, colorless and confluent within. Cells short barrel-shaped, 3.0–3.5μ in diameter. Heterocysts almost spherical, cir. 6μ in diameter. Resting cells elliptical, cir. 5μ in diameter by cir. 7μ in length, with smooth, yellowish membranes.

This cosmopolitan plant has been found in standing and flowing water, attached and (later) free-floating, in numerous places in North America. While it has not been previously noted in the Yellowstone Park, it has been found in Montana (Anderson and Kelsey).

It is very common in non-thermal waters in the Park, and occasional in slightly warmed waters. In two sites in the Upper Geyser Basin and in one in the Biscuit Basin it occurred at cir. 30.2°C. (highest temperature noted 31.2°C.). The alga is distinctly non-thermal and is not well developed at above 25°C.

CYLINDROSPERMUM Kütz

Phyc. gen., p. 211, 1843.

Plant mass indefinite, formless, slimy, usually dark blue-green. Trichomes uniform throughout their length. Sheaths absent; filaments imbedded in a homogeneous, difficulty visible, very soft slimy matrix, straight, flexuous, or contorted, never spirally coiled, mostly short; free filaments ("hormogonia") feebly motile. Cells cylindrical, rounded at the ends. Heterocysts mostly single, terminal at both ends of the trichomes, or following breakage at a single end only. Resting cells single or in a few species in rows, sometimes

in twos, adjacent to the heterocysts (subterminal), often at both ends of trichomes; much larger than the vegetative cells. Pseudovacuoles absent (always ?).

The species live either in fresh water or on moist soil, etc. A few occur in slightly brackish water. No thermal forms have been previously noted. The genus has not been previously credited to the Yellowstone.

In the Park the genus is moderately well represented but is not especially important. Two species, *C. licheniforme* Kütz. and *C. maius* Kütz., have been noted exclusively in non-thermal situations; two others have been found in thermal waters as well. The non-thermal forms are not included below.

KEY TO THE YELLOWSTONE SPECIES.

I. Resting cells single, with yellowish brown membranes; cells 3.8–4.5μ in diameter.   *C. stagnale* 1.
II. Resting cells in rows, with colorless membranes; cells cir. 2.7μ in diameter.
                                                                    C. marchitum 2.

1. CYLINDROSPERMUM STAGNALE (Kütz.) Born. & Flah.

Rév. Nostoch. hét. 4, p. 250, 1888.

Stratum extended, floating and flocculent or attached and flocculent to soft-gelatinous; dark blue-green, occasionally brownish. Cells almost quadrate to cylindrical, constricted at the cross walls, 3.8–4.5μ in diameter by 1.2–2.5 diameters in length, pale blue-green. Heterocysts spheroidal to elongate, sometimes somewhat conical with rounded end, 6–7μ in diameter by up to 16μ in length. Resting cells cylindrical with rounded ends, 10–16μ in diameter by 32–40μ in length, single, with smooth yellowish-brown membranes.

Cosmopolitan and abundant, and well known in North America, the species grows in standing or slowly flowing fresh water, attached to the bottom or to water plants, or floating, or on moist soil, rocks, etc. It has not been previously noted in the Yellowstone.

Found generally in its usual habitats in the Yellowstone, it also invades thermal sites to a striking degree. Its greatest abundance was noted in the crater of Imperial Geyser, Twin Buttes Region (no. 320). There it grew at temperatures up to 44.1°C., on wet sinter below a seep in the wall of the crater. The water from the seep was slightly acid. The plants bore spores in considerable abundance in the warmest places it inhabited, and the growth was normal and typical.

2. Cylindrospermum marchitum Lemm.

Krypt.-Fl. Mark Brandenb. 3, p. 196, 1910.

Syn.: *Cylindrospermum catenatum* var. *marchitum* Lemm.

Stratum bright blue-green. Cells quadrate to cylindrical, constricted at the cross walls, cir. 2.7μ in diameter by 2.7–5.5μ in length; cell contents blue-green. Heterocysts elongate, cir. 2.7μ in diameter by cir. 5.5μ in length. Resting cells in rows, elongate with rounded ends, often slightly curved, with smooth, colorless membranes, 4.5–5.5μ in diameter by 12–16μ in length.

Known only from North Germany and Latvia, the presence of this species in the Yellowstone is surprising. It has been found growing on moist earth in both of its localities.

It has been noted in the present investigation only in the Twin Buttes Region, in seeps in the crater of Imperial Geyser (no. 320). The strata grew on moist, warm sinter and earth at 26-41°C., kept wet with water of a slightly acid reaction. Locally the alga was frequent, and in the majority of the filaments studied spores in catenate series of up to eight were found. It was accompanied by *C. stagnale* (Kütz.) B. et F., *Chroococcus minutus* var. *thermalis* (of this paper), *Mastigocladus laminosus* var. *anabaenoides* Boye Pet., *Nostoc entophytum* B. et F., *Microspora* sp. and *Cosmarium* sp. The growth was more abundant in the lower part of its temperature range and apparently it is a facultative transitional form.

OSCILLATORIACEAE (Gray) Kirchner

Engler-Prantl, Nat. Pflanzenf. I 1 a, 1900.

Key to the Yellowstone Genera.

I. Trichomes without sheaths, or with very thin and scarcely visible sheaths.
  1. Trichomes straight, flexuous, or irregularly coiled.
        Oscillatoria (p. 140)
  2. Trichomes regularly spirally twisted.
    A. Trichomes with cross walls visible in life.   Arthrospira (p. 160)
    B. Trichomes with cross walls visible only with special staining.
      a. Cell wall rigid; locomotion normal.   Spirulina (p. 161)
      b. Cell wall flexible; locomotion spirochaete-like.
        Glaucospira (p. 165)
II. Trichomes with sheaths present; sheaths of perceptible thickness, visible at least in places.
  1. Sheaths containing mostly a single trichome.
    A. Sheaths thin or of moderate thickness, not very thick.
      a. Sheaths slimy, mostly confluent (at least in part).
        *. Filaments united into a simple resupinate stratum; stratum plane, hydnoid, wrinkled, or papillate to columnar above, unspecialized below.   Phormidium (p. 166)

**. Filaments united into a complex laterally attached stratum; plane to wrinkled above, fimbriate below.
                                        CYANOHYDNUM (p. 199)
  b. Sheaths firm, not confluent or feebly so (stratum often gelatinous).
    *. Filaments prostrate below, united into erect hydnoid fascicles or tufts above; often with feebly confluent sheaths.
                                        SYMPLOCA (p. 195)
    **. Filaments single or united into a stratum with the filaments mostly similarly placed throughout, without well-developed fascicles.
        !. Filaments single or united into tufts, or into a pilose, fibrous or tufted stratum.   LYNGBYA (p. 189)
        !!. Filaments always united into a membraneous stratum, closely packed, interwoven.   SCHIZOTHRIX (p. 200)
  B. Sheaths very thick, inner layers firm and mostly golden-brown, outer soft and irregular and colorless.   POLYCHLAMYDUM (p. 194)
2. Sheaths containing mostly a few to many trichomes.
  A. Sheaths firm, not at all or feebly slimy.
    a. Trichomes close together in the sheath.   SCHIZOTHRIX (p. 200)
    b. Trichomes distinctly separated in the sheath.
                                        DASYGLOEA (p. 205)
  B. Sheaths slimy, soft.   MICROCOLEUS (p. 206)

OSCILLATORIA Vaucher

Hist. Confer. d'eau douce, p. 165, 1803.

Incl.: TRICHODESMIUM Ehrenberg.

Filaments naked or rarely with delicate, fugitive sheaths, single or united into free-floating flocculae, or forming indefinite masses or strata. Trichomes mostly motile, with a rotatory creeping motion. Trichome apices simple or modified. Hormogonia produced by fragmentation of the trichomes, often brought about by death of unspecialized cells (the biconcave refringent cells). Pseudovacuoles often present; sulphur granules present in a few species. Color of protoplasts variable, blue-green, olive-green, reddish, steel-blue, yellowish, and almost colorless. Resting cells unknown.

The numerous species of this very large genus are found in most habitats in which the Myxophyceae occur. The genus is best represented in submerged and very wet situations. The various species are found in fresh, brackish, salt, acid, sulphide-containing, and hot waters. The taxonomy of the group is difficult and in part artificial.

Several species regularly occur in thermal springs. The following have been reported from warm and hot water in North America: *O. princeps* Vauch., *O. sancta* Kütz., *O. tenuis* Kütz., *O. amphibia* Ag., *O. acuminata* Gom., *O. Cortiana* Menegh., *O. numidica* Gom., *O. Boryana* (Ag.) Bory,

O. geminata Menegh., and *O. Ulrichii* Prát.   Of these *O. princeps, O. geminata, O. amphibia,* and *O. Ulrichii* have been noted in the Yellowstone (Weed, 1897, Tilden, 1910, Prát, 1929).   Other thermal species include *O. proboscidea* Gom. and its var. *Westii* Forti, *O. anguina* (Bory) Gom., *O. chalybea* Mert., *O. terebriformis* Ag., *O. animalis* Ag., *O. Okeni* Ag., *O. formosa* Bory, *O. ornata* Kütz., *O. subbrevis* Schmidle, *O. jasorvensis* Vouk, *O. angustissima* W. & G. S. West, and *O. splendida* Grev. and its var. *Füllebornii* Schmidle.

In the present study twenty-nine species and varieties have been encountered, making *Oscillatoria* the largest genus of Yellowstone Myxophyceae.   The species occur in water up to 85.2°C.   (*O. filiformis* of this paper), and are best represented in feebly acid, neutral, and basic waters. In strongly acid water the genus is unimportant.   In general the species, while abundant in the great majority of the springs, are more or less incidental, and the genus is secondary in importance to *Phormidium*.   It may be compared to *Synechococcus* in its place in the springs.   The several species are so varied ecologically that it is difficult to draw any general conclusions concerning their distribution.   While some of the species are strictly thermal, and one is limital, the majority are apparently either transitional or facultative in their temperature relationships.   It is notable that a large proportion of the Yellowstone species are world-wide in distribution, or are at least known from other continents.   This is in sharp contrast to such other genera as *Calothrix* and *Synechococcus,* both of which include a large proportion of apparently endemic species.

<center>KEY TO THE YELLOWSTONE SPECIES.</center>

I. Cells short, not more than one third diameter in length.
  1. Trichomes not constricted at the cross walls.
    A. Trichome apices straight.   *O. limosa* 1.
    B. Trichome apices curved or bent.
      a. Trichomes 6–8μ in diameter.   *O. anguina* 2.
      b. Trichomes 16μ or greater in diameter.
        *. Cells with normal pigmentation.
          !. Trichomes 29–42μ in diameter.   *O. princeps* 3.
          !!. Trichomes 16–21μ in diameter. *O. princeps* var. *tenella* 3A.
        **. Cells very pale, almost colorless. *O. princeps* var. *pallida* 3B.
  2. Trichomes contricted at the cross walls.   *O. sancta* 4.
II. Cells of moderate length, one third diameter or greater.
  1. Cells with pseudovacuoles.   *O. lacustris* 5.
  2. Cells without pseudovacuoles.
    A. Trichome apices straight.
      a. Trichome apices neither capitate nor calyptrate.
        *. Trichome 1.4μ or greater in diameter.

!. Trichomes not constricted at the cross walls.

    ‡. End-cell rounded.   *O. amphibia* 7.

    ‡‡. End-cell pointed.   *O. amphibia* var. *Acus* 7A.

!!. Trichomes constricted at the cross walls.

    ‡. Cells as long as or longer than their diameters.

        x. Trichomes 1.7–4μ in diameter; cross walls thick.

            $. Trichomes 2.2–4$\mu$ in diameter.

                ∅. Filaments moderately long, mostly many-celled.   *O. geminata* 23.

                ∅∅. Filaments mostly less than 10-celled.

                    O. geminata var. *fragilis* 23A.

            $$. Trichomes 1.7–2μ in diameter.

                    O. geminata var. *tenella* 23B.

        xx. Trichomes cir. 1.5μ in diameter; cross walls thin.

                    O. limnetica 6.

    ‡‡. Cells one diameter or less in length.

        x. Trichomes 3.4–4.2μ in diameter; filaments short and few-celled; deeply constricted at the cross walls.   *O. Jovis* 24.

        xx. Trichomes 4–10μ in diameter; filaments many-celled; lightly constricted at the cross walls.

        $. Stratum thin, olive to blue-green.

                    O. tenuis 10.

        $$. Stratum thick, dark olive to blackish.

                    O. nigra 11.

**. Trichomes 0.7μ or less in diameter.

    !. Trichomes 0.6μ in diameter; cells cir. two diameters in length; stratum blue-green.   *O. angustissima* 8.

    !!. Trichomes 0.4–0.5μ in diameter; cells cir. three diameters in length; stratum tannish.   *O. filiformis* 9.

b. Trichome apices capitate and calyptrate.   *O. amoena* 12.

B. Trichome apices curved, bent, or twisted at least slightly.

a. Trichome apices capitate.

    *. Cells cir. one diameter in length; trichome apices conical.

        !. Filaments not spirally twisted; trichomes lightly constricted at the cross walls.   *O. amoena* 12.

        !!. Filaments spirally twisted, at least at apical ends; trichomes not constricted at the cross walls.

                  O. beggiatoiformis var. *maxima* 15A.

    **. Cells 2–4 diameters in length; trichome apices rounded.

                    O. splendida 13.

b. Trichome apices not capitate.

    *. Trichomes not constricted at the cross walls.

        !. Trichomes 4–6.5μ in diameter.   *O. terebriformis* 14.

        !!. Trichomes 2–2.5μ in diameter.   *O. Lemmermannii* 17.

    **. Trichomes constricted at the cross walls, often only slightly.

        !. Filaments spirally twisted at least in apical portions.

                    O. Boryana 16.

!!. Trichomes not spirally twisted, often curved at apices, often flexuous throughout.

 ‡. Trichomes not tapering at apices.

  x. Stratum thin, olive to blue-green.   *O. tenuis* 10.

  xx. Stratum thick, dark olive to blackish.   *O. nigra* 11.

 ‡‡. Trichomes tapering at apices.

  x. Trichomes lightly to moderately constricted.

   $. Cells near apices longer than those remote from ends.

    ø. Cells 1/3–2/3 (up to 1) diameter in length.

             O. Okeni 18.

    øø. Cells cir. one diameter in length.

             O. Cortiana 19.

   $$. Cells near apices of same length as those remote from ends.

    ø. Trichomes 4–6μ in diameter; cells cylindrical.   *O. formosa* 20.

    øø. Trichomes 5–8μ in diameter; cells feebly swollen. *O. chalybea* var. *depauperata* 21.A.

  xx. Trichomes very deeply constricted at the cross walls.

             O. Ulrichii 22.

1. OSCILLATORIA LIMOSA Agardh

Disp. Alg. Succ., p. 35, 1812.

Stratum dark blue-green to brown, extended, attached at first and later free-floating, up to 1 cm. in thickness. Trichomes mostly straight, not constricted at the cross walls (often feebly constricted in poorly preserved material), 11–22μ in diameter (mostly 13–16μ). Cells 1/6–1/3 diameter in length, 2–5μ long; cross walls usually granulated. Trichome apices straight, not at all or feebly tapering, end cells blunt but convex, end membranes slightly thickened, apices not capitate. Cell contents blue-green to olive.

This is one of the most abundant of the numerous species of *Oscillatoria*. It is cosmopolitan and has been recorded from numerous localities in the United States, as well as elsewhere. It occurs in standing or slowly flowing fresh water, less often in polluted or mildly brackish water, and rarely on damp mud, wet rocks, etc. It is frequently found stranded on muddy pond and stream edges, but does not ordinarily grow there. It is found in abundance throughout the year, and is not injured by alternate freezing and thawing.

In the Yellowstone it does not seem to be abundant, possibly because there are few bodies of more or less stagnant and slow-flowing water. It has been noted in the Gibbon and Firehole rivers in quiet pools, and in a few warm springs at low temperatures. The springs in which it was noted include: White Elephant Grottoes, Mammoth Hot Springs (24.6° C.); pools at West Thumb (up to 29.2°C.); and pools in the Lower Geyser

Basin (up to 23.5° C.). The plant is obviously non-thermal and tolerates temperatures no higher than encountered in shallow pools in regions without any thermal influence.

2. OSCILLATORIA ANGUINA (Bory) Gomont

Monogr. Oscill., p. 214, 1892.

Stratum dark blue-green, slimy-membranous, blue-black when dried. Trichomes straight, at apices spirally twisted and gradually and distinctly tapering, not constricted at the cross walls, frequently with swollen, biconcave refringent cells, 6–8μ in diameter. Trichome apices capitate, rounded or obtusely flattened, end walls sometimes slightly thickened. Cells 1/6–1/3 diameter in length, 1.5–2.5μ long, cross walls sometimes granulated; cell contents blue-green.

Known from several localities in the United States, and from Europe, Africa, Java, Iceland, and elsewhere; it occurs in quiet waters, polluted water, on moist mud, and in warm springs. In North America it has been reported from non-thermal sites only.

Previously unknown but apparently quite frequent in the Yellowstone, it is found chiefly in non-thermal waters. It has been noted in slowly flowing portions of the Firehole River, and in seven springs in the Upper and Lower Geyser Basins. Its temperature range, as observed, was from 14 to 36.8°C.; it was found only in basic waters, pH. 8.2-8.85.

3. OSCILLATORIA PRINCEPS Vaucher

Hist. Conferves d'eau douce, p. 190, 1803.

Plant mass dark blue-green to bluish-black, slimy. Trichomes mostly straight, rigid, not constricted at the cross walls, 29–42μ in diameter, pale or bright blue-green to olive-green. Apices slightly narrowed, feebly curved, subtruncate. Cells 1/11–1/4 diameter in length (3.5–7μ); traverse walls not granulated, end cell somewhat capitate, with an unthickened or slightly thickened wall. Cell contents finely granular or occasionally with prominent granules.

Oscillatoria princeps Vaucher, as described in the literature, is an extremely variable species, particularly so in size. It is usually listed as varying from 16–60μ in diameter. Single collections of the plant show, in general, only a moderate size range. It is probable that the "species" is a "species complex" or a plexus of closely allied but more or less distinct varieties. Geitler (1925) states that: "Die Art umfasst zweifellos mehere gute Arten, die durch ihre Grösse (und wahrscheinlich auch andere Merkmale) voneinander verschieden sind." I am restricting the name *O. princeps* Vaucher to the form that varies from 29 to 42μ in diameter, and that is found in quiet flowing or standing water, either floating or

on the bottom. The species, in this restricted sense, is cosmopolitan and quite common—probably more abundant than any of its varieties. In the Yellowstone I have found *O. princeps* only in non-thermal waters. It was found in a small pond near the Mammoth Hot Springs in 1928, and in the Firehole River in a shallow, sluggish portion, near the Lower Geyser Basin, in 1931. Tilden (1898) records *O. princeps* from thermal springs in the Yellowstone. Specimens distributed by her fall in the variety *tenella* described below.

3A. OSCILLATORIA PRINCEPS Vaucher

var. tenella var. nov.

Plant mass blue-black. Trichomes 16–21μ in diameter. Cells ranging from 1.2 to 2.4μ in length, bright blue-green to olive-green. Hormogonia numerous, 20–40μ in length. Otherwise as in the species.

The variety *tenella* is the common Yellowstone thermal form of *O. princeps*. Tilden (1898) records it (as *O. princeps* Vaucher) from the Lower and Upper Geyser Basins in unnamed but well-described and accurately located springs. She found it at temperatures ranging from 38 to 42°C., and somewhere between 19° and 58°C. (?). I have found it in the Upper and Lower Basins; in the Twin Buttes Region, and in the Roaring Mountain and Meadow Springs Region. The type (no. 187) is from one of the Meadow Springs (cir. one-quarter mile north of Semi-centennial Geyser), at a temperature of 48°C. and pH. 6.65. In this site it almost filled a small pond with a blue-green slimy stratum, and nearby it was found in several other springs and spring rills. In other sites it occurred at temperatures from 31°C. to 56°C. and at acidities ranging from pH. 6.5 to 8.3.

3B. OSCILLATORIA PRINCEPS Vaucher

var. pallida, var. nov.

Filaments scattered among other algae. Trichomes flexible, 18–30μ in diameter, pale gray to pale olivaceous, very long. Hormogonia few and long, over 100μ in length. Cells 3–7μ in length, cell contents with a few conspicuous granules. Otherwise as in the species.

This variety overlaps the size range of *O. princeps* forma *tenuior* Rabenh. but is quite distinct in color and presents a greater variation in size. (Rabenhorst gave a brief and rather non-critical description that did not clearly define his form.) The very pale color and deficient supply of chlorophyll at first suggested that the specimens were abnormal and diseased. This is improbable. The pallid filaments did not occur with *O. princeps* or its var. *tenella,* but were in distribution totally distinct.

The filaments were actively motile and strikingly flexible, these characters being much more pronounced than in the forms with normal pigmentation. Isolated filaments were kept in tubes for several days and not only remained alive but grew in length. The pallid characteristic was constant in all localities where the plant was found. The physiology of this variety should be of considerable interest; it is possible that it is sapropeltic.

The plant is not common. The most abundant collection (type: no. 443) was from the Firehole River, Upper Geyser Basin, at the point of entrance of a hot spring overflow, growing at 32.2°C. and pH. 8.8. The plant was found in four other sites in the same vicinity in basic waters (pH. 8.4–9.0) and at moderate temperatures (26–34°C.).

4. OSCILLATORIA SANCTA Kütz.

Tab. Phyc., 1, p. 30, 1845-1849.

Plant mass thin, blue-black, shining, slimy-gelatinous. Trichomes long, straight, flexuous or lightly contorted, 10–20μ in diameter, distinctly constricted at the cross walls, apices slightly tapering, straight. Cells 1/3–1/6 diameters in length, 2.5–6μ long; cross walls with numerous granules; cell contents olive-green to dull blue-green. End cell flattened-hemispherical, feebly capitate, with a thickened wall.

Occurring commonly in standing water, floating or benthonic, occasionally in flowing water and on damp woodwork, rocks, etc., *O. sancta* is known from almost all over the earth. In the United States it has been reported from New York to California. (It is possible that most of the records of *O. sancta* from emersed situations should be referred to the varieties *caldariorum* (Hauck) Lager. and *aequinoctialis* Gom.). Harrison reported the species from a warm spring at Lebanon Springs, New York. It is not frequent in thermal situations.

In the Yellowstone I have found *O. sancta* in non-thermal pools quite frequently. In the Firehole River at the Upper Geyser Basin (no. 432) it occurs in water warmed to 22.5°C. by hot spring overflows. At this place the water has a pH. of 8.2. I regard the species as a non-thermal type, invading very slightly the edges of certain thermal situations. The trichomes of the Yellowstone material vary from 10–17μ in diameter.

5. OSCILLATORIA LACUSTRIS (Kleb.) Geitler

in Pascher, Die Süsswasserflora 12, Cyanophyceae, p. 362, 1925.

Syn.: *Trichodesmium lacustre* Kleb.

Trichomes straight or sometimes slightly curved, united into flocculent, dust-like free-floating bundles. Cells short barrel-shaped, 5–7μ in diameter

by 3–7μ in length, with numerous pseudovacuoles. Apices straight, not taper-
ing. End cell frequently elongate, subcylindric, tapering slightly, with a
rounded apex.

O. lacustris is a typical planktonic *"Trichodesmium."* It does not
have the capitate apices characteristic of many of them but the flocculae
into which the pseudovacuole-filled trichomes are united are quite char-
acteristic. Typical *O. lacustris* has not been previously reported from
North America. Smith found, in a lake in Wisconsin, a form of *O.
lacustris* with the end cells not elongate, but otherwise quite typical.

In the Yellowstone *O. lacustris* is not common. I have found it as a
plankton component in the Firehole River at the Upper Geyser Basin
(no. 432), in water at from 22.5° C. to 26° C., with a pH. of 8.2. This
temperature is below that frequently found in the surface waters of non-
thermal lakes and ponds. The species, although in water clearly modified
by the nearly thermal springs, is non-thermal in its essential relationships.

6. OSCILLATORIA LIMNETICA Lemmermann

Ber. deutsch. Bot. Ges., p. 310, 1900.

Trichomes straight or almost so, distinctly constricted at the cross walls,
pale blue-green, cir. 1.5.μ in diameter. Cells 2.5–8.0 diameters in length, 4–12μ
long. End cells rounded, apices unspecialized.

Occurring widely in the surface waters of pools and lakes, often in
polluted water, and among other algae, it has up to now been known
neither from the United States nor from thermal habitats. It is un-
doubtedly present throughout central United States, and is not so un-
usual as the former lack of published records indicates. The author has
found the plant in Crescent Lake, Richmond, Indiana, and in a pond
near Ravenna, Nebraska.

In the Yellowstone it has been noted only in Soda Spring, Mammoth
Hot Springs (no. 127). In this peculiar spring (with a high mineral
content) it grew at 30–31° C., pH. 6.5, along with *Chroococcus turgidus*
(Kütz.) Naeg. var. *thermalis* (Kütz.) Rab., *Oscillatoria angustissima*
W. & G. S. West, *O. geminata* Menegh., *O. amphibia* Ag., and *Beggiatoa
minima* Warming. The alga gave little evidence of being truly thermal.

7. OSCILLATORIA AMPHIBIA Agardh

Flora 10, pt. 2, p. 632, 1827.

Plant mass clear blue-green. Trichomes straight or flexuous to twisted, not
constricted at the cross walls, 2–3μ in diameter; cell contents pale blue-green.
Cells 2–3 diameters in length, 4–9μ long, cross walls usually with a prominent

granule on each side, apices unspecialized, neither capitate nor calyptrate, not tapering, end cell rounded.

Cosmopolitan in standing water, in brackish, polluted, and warm waters, and on moist earth in greenhouses, it is widely distributed in North America. Wolle (1877) reported it (locality unmentioned) from wet wood subjected to factory waste at cir. 100° F. (37.8° C.), and Tilden (1898) recorded its presence in the Yellowstone Park, Upper Geyser Basin, in the channel of a spring above Beehive Geyser (temperature?). It is interesting that the species was originally found by Agardh at Carlsbad, Bohemia, in thermal waters at 36–44° R.

In the Park *O. amphibia* is widely distributed but apparently rare. It has been noted in the Mammoth Hot Springs: White Elephant Grottoes (no. 90), at 49° C., Jupiter Terrace (nos. Y2, Y9); Meadow Springs: small pool (no. 187); Upper Geyser Basin: Bijou Geyser (no. 439), at 36.8° C., pH. 8.95, seep on bank of Firehole River near Midway Basin, at 41° C., pH. 8.4; and in the Lower Geyser Basin: seep near Great Fountain Geyser, at 27° C., pH. 8.35. It gives no evidence of enduring high temperatures and may be considered as a transitional form.

7A. Oscillatoria amphibia Agardh

var. Acus, var. nov.

Plant mass brilliant blue-green; trichomes bright blue-green, 2.3–3.0µ in diameter, straight or flexuous, not constricted at the cross walls. Cells 2–3 times as long as broad, and mostly with two granules at the inconspicuous cross walls. End cell without calyptra, obtusely pointed at apex.

The variety *Acus* differs from *O. amphibia* Agardh chiefly by having pointed rather than rounded apices.

Its range in the Yellowstone is quite distinct from that of the species. *O. amphibia* var. *Acus* favors the basic siliceous waters of the Geyser Basins while the *O. amphibia* was found most abundantly at Mammoth. The type (no. 441) was collected in the Firehole River at the point of entrance of Bijou Geyser overflow and a small hot spring. At this site the temperature was 55.8° C. and the pH. was 8.85. It has been found in several springs in the Upper, Midway, and Lower Geyser Basins at temperatures from 37.3° C. to 61.7° C., always in basic waters, pH. 8.2–9.05.

8. Oscillatoria angustissima W. & G. S. West

Jour. Bot. 35, p. 300, 1897.

Stratum extended, blue-green. Trichomes 0.6µ in diameter, long, flexuous and tangled, not constricted at the cross walls, clear blue-green, apices not

tapering, apical cell rounded, neither capitate nor calyptrate. Cells 1.3–2.4 diameters in length, 0.8–1.5µ long, cross walls indistinct.

Known from standing water, sulphur springs, and warm springs in Europe, South Africa, and North America, this plant has probably often been overlooked because of its small size. In the United States it has
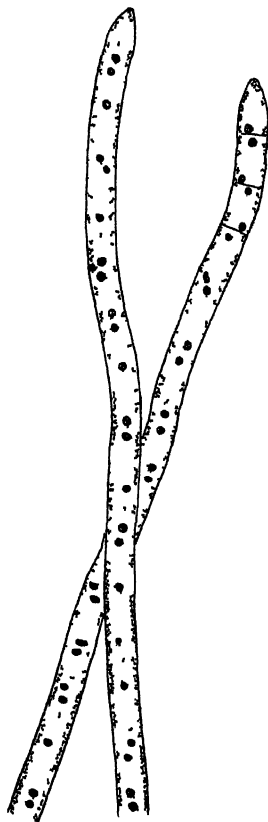
Fig 55.—*Oscillatoria amphibia* var. *Acus* (×1540).

been noted in non-thermal waters in Iowa (Buchanan, 1908) and Missouri (Drouet, 1932).

In the Yellowstone it is common but rarely abundant in the Mammoth Hot Springs and is infrequent elsewhere. It has been found at Mammoth in Angel Terrace, Jupiter Terrace, Diana Terrace, Hymen Terrace, White Elephant Grottoes (nos. 97, 98, 100, 101), Orange Spring Mound, and Narrow Gauge Terrace; in the Chocolate Pots (Gibbon

River valley) (no. 274); in the Upper Geyser Basin: unnamed spring; and in the Meadow Springs: a small pool (no. 187). Its observed temperature range is 31–57.3° C., its pH. range 6.0–7.3.

9. Oscillatoria filiformis, sp. nov.

Plant mass salmon-brown to tannish. Trichomes long, flexuous, entangled, 0.4–0.5μ in diameter, not constricted at the cross walls, pale dull blue-green, apices not tapering. Cells cir. 3 diameters in length, 1.0–1.6μ long, cross walls mostly visible, end cells neither capitate nor calyptrate.

This extremely minute *Oscillatoria* is close to *O. angustissima* W. & G. S. West. It is separated from it by its more slender trichomes, longer cells, and brownish stratum.

The type (no. 327) is from the Twin Buttes Region, Imperial Geyser overflow, at 60° C., and pH. 8.85. It has been noted in several springs in some abundance and is apparently quite common in the Lower and Upper Geyser Basins. Its observed range includes the Artist's Paint Pots: small pool (no. 297), at 85° C.; Meadow Springs: small spring (no. 180), at 85.2° C., pH. 7.4; Twin Buttes Region: Spray Geyser (no. Y80), Imperial Geyser Crater (nos. 322, 326), at 64° C. and 69.4° C., pH. 8.8, Imperial Geyser overflow (nos. 325, 327), at 60° C. and 65° C., pH. 8.85 and 8.8. In general it grows on and among other Myxophyceae or at the higher temperatures alone. It is one of the most typical limital species of the basic springs. The temperature of 85.2° C. which it tolerates may be a fraction of a degree above the limit for growth. In the Meadow Spring it was not possible to check the constancy of the temperature for a satisfactory time. In the Artist's Paint Pot spring it was growing at 85° C. Only a single other species, *Phormidium bijahensis* (of this paper), was found that endured the temperature of 85° C. That species was found growing in water that did not fall below 85.2° C. The species, from all evidence at hand, is restricted to strictly thermal waters.

10. OSCILLATORIA TENUIS Agardh

Algarum Decades 2, p. 25, 1813.

Plant mass thin, slimy, bright blue-green to olive-green. Trichomes straight, fragile, lightly constricted at the cross walls, 4–10μ in diameter, cell contents pale blue-green; trichomes not tapering at the apices, but often curved. Cells 2.5–5μ long, mostly granulated at the cross walls; end cells more or less hemispherical, broadly rounded, not capitate but with a lightly thickened end wall.

Cosmopolitan in standing water, attached or floating, less often in polluted and warm water, it has been reported from numerous localities in North America, ranging from Greenland and the Arctic to the West Indies.   Tilden (1898) reported it from "a small mountain spring in a bog, together with moss and water cress," Lower Geyser Basin, Yellowstone Park.   Since water cress is absent in even warm springs, she must have found the plant in cool water.   There are no previous thermal records for it in this hemisphere.

In this investigation it has been found a single time in thermal waters, and several times in non-thermal situations.   The spring in which it was noted was in the Bijah group about 20 feet south of Bijah Spring (no. 120), at 27° C., pH. 6.0.

11. OSCILLATORIA NIGRA Vaucher

Hist. Conferves d'eau douce, p. 192, 1803.

Plant mass membranaceous, often floating, dark olive-green to lead-colored, glistening.   Trichomes straight or feebly flexuous, 6.0 to 10μ in diameter, lightly constricted at the cross walls; apices not tapering but with obtusely conical end cells.   Cells 0.4–1.0 diameter in length, cross walls granulated; cell contents finely granular, pale olivaceous; end cells neither capitate nor calyptrate (often "bearded" with epiphytic bacteria).

Known from standing and slowly flowing water and wet rocks, *O. nigra* has been reported from Europe and North America.   It has not been credited to thermal habitats, and has not been previously reported from the Yellowstone.

It has been found, in the Park, only in Ochre Springs (no. 62), at 36° C., pH. 6.0.   Ochre Springs is a small boggy, alga-choked, tepid spring group on the slope of Elephant Back Mountain, overlooking the Yellowstone River, a few miles south of Yellowstone Lake.

12. OSCILLATORIA AMOENA Gomont

Monogr. Oscill., p. 225, 1892.

Stratum dark bluish-green.   Trichomes straight, feebly flexuous, very slightly constricted at the cross walls, 2.5–5μ in diameter, gradually tapering toward the often undulate apices, dark blue-green.   Cells 2.5–4.2μ long, almost isodiametric, cross walls granulated; end cells somewhat longer than the trichome cells, both capitate and calyptrate, with broadly conical apices.

Growing in standing warm and cool waters on water plants, stones, etc., it is known from North America, Europe, and Africa.   In the United States it has been reported from Massachusetts (Collins, 1896),

Connecticut (Hylander, 1928), and Missouri (Drouet, 1932). Saunders (1901) recorded it from Sitka, Alaska, where it grew in the channel of a hot spring overflow at 80–120° F. (26.8–48.9° C.).

In the Park it is common in cool water: Gardiner River at Five Mile Bridge (no. 195), at 10.5° C.; Rustic Falls on Glen Creek (nos. 152, 154), at 15° C., pH. 8.5; and elsewhere. In some streams warmed by thermal waters it is frequent but it has not been observed in warm water. The site in which it was found at the highest temperature was in the Firehole River above the rapids (no. 337), at 17.8° C., pH. 7.2.

13. OSCILLATORIA SPLENDIDA Greville

Flora Edinensis, p. 305, 1824.

Plant mass thin and tenuous or thicker and membranous; brilliant blue-green to olive-green. Trichomes straight to flexuous, not constricted at the cross walls, gradually tapering toward the apex, 2–3μ in diameter. Apices more or less twisted or bent, tapering, capitate, with a swollen almost globose apex, without calyptra. Cells 2–4 diameters in length, 3–9μ long, usually granulated at the cross walls; cell contents blue-green.

Occurring in standing fresh, brackish, and polluted waters, and in warm springs, it is cosmopolitan and common. In the United States it is very well known.

Although not previously reported, it might well have been expected in the Park. It has been found in the cooler waters of several springs at temperatures up to 31.4°C. In general it is more abundant in neutral to basic waters (pH. 6.6-8.5), and is commoner in cool water. It was noted in the greatest abundance in Lily Pad Lake (non-thermal), at 19.5°C., pH. 7.55 (no. 171).

14. OSCILLATORIA TEREBRIFORMIS Agardh

Flora 10, p. 634, 1827.

Plant mass dark lead-colored. Trichomes 4–6.5μ in diameter, flexuous, loosely spiraled and terebriform above, gradually and slightly tapering toward the apex, not constricted at the cross walls. Cells 0.5–1.0 diameter in length, 2.6–6.0μ long. End cell rounded or almost truncate, neither capitate nor calyptrate; cross walls often granulated.

Known from hot and sulphur springs in many localities in Europe and Africa, and from standing cool water and wet rocks in diverse regions, this species is probably cosmopolitan. In the United States it is known only from Massachusetts (Collins, 1896) and Connecticut (Hylander, 1928).

In the Yellowstone it is widely distributed but probably rare. It has been found in three sites only. These include Mammoth Hot Springs: Jupiter Terrace overflow (no. Y2) at 28°C., pH. 7.8; Twin Buttes Region: Fairy Creek at source (no. 413), at 42°C., pH. 8.1; and Upper Geyser Basin: seep on bank of Firehole River opposite Geyser Hill, at 32°C., pH. 8.05.

15A. OSCILLATORIA BEGGIATOIFORMIS (Grun.) Gom.

var. maxima, var. nov.

Filaments free among other algae. Trichomes very pale blue-green to dull olive-green, very long, mostly straight to flexuous, often loosely spirally twisted, especially toward the apices, not constricted at the cross walls, 6–9μ in diameter, distinctly and gradually tapering at the apices. Cells quadrate or slightly shorter or slightly longer than their diameters, 5–11μ in length; distinctly granulated at the cross walls. End cell capitate, with an obtusely conical, bluntly pointed calyptra.

O. beggiatoiformis maxima can be characterized as a solitary, oversized strain of *O. beggiatoiformis* (Grun.) Gom. The cells are proportionally more variable in size, considerably larger, and the trichomes are less torulose, taper to a less narrow tip and are broader than in the species. The whitish, lime-encrusted stratum of *O. beggiatoiformis* is sharply lacking in var. *maxima.*

This plant has been found in the Firehole River in places where the water is warmed slightly by hot springs. The type (no. 432) is from the Upper Geyser Basin opposite the Biscuit Basin, growing at 22.5°C. and pH. 8.2. Apparently the variety is rare and local in the Yellowstone. It is probably a non-thermal type, but seems to be favored by water in the low twenties.

16. OSCILLATORIA BORYANA (Ag.) Bory

Dict. class. d'hist. nat. 12, p. 465, 1827.

Plant mass dark lead-colored. Trichomes loosely and regularly spirally twisted throughout their length or only toward the apex, flexuous, very lightly constricted at the often lightly granulated cross walls, 6–8μ in diameter. Apices more or less pointed with end cells narrowly rounded to pointed, neither capitate nor calyptrate. Cells 0.5–1.0 diameter in length, 3–7μ long, with usually granular contents.

Growing in hot springs in North America, Europe, and Africa, it has not been previously reported from the United States. Kellerman (Tilden, 1908) collected it in a warm stream in Guatemala, where it formed a dark velvety stratum.

FIG. 56.—*Oscillatoria beggiatoiformis* var. *maxima* (×530).

In the Yellowstone it is apparently rare. It has been found only at the Mammoth Hot Springs: White Elephant Grottoes (nos. 96, 99), in abundance at 38–23.5°C., growing on wet travertine; and in Jupiter Terrace runoff (no. OS40), at 30° C., pH. 7.7.

17. Oscillatoria Lemmermannii Wolosz.

Bull. Ac. Sc. Cracovie, S. B., p. 687, 1912.

Plant mass blue-green, slimy, often occurring as single filaments. Trichomes pale blue-green, straight or somewhat contorted, not constricted at the cross walls, 2.0–2.5μ in diameter, apices curved and distinctly tapering. Cells 2–3 diameters in length, 4–6μ long; cell contents homogeneous; cross walls finely granulated. End cell tapering and curved with a rounded unthickened end wall.

The only previous record for *O. Lemmermannii* is from lakes in Java, where it occurs as a plankton component (and possibly otherwise?).

Its occurrence in the Yellowstone, while unexpected, is not surprising. It was found in floating masses of algae in a quiet pool at the edge of the Firehole River, Upper Geyser Basin, in tepid water. The temperature range in which it was growing was cir. 27–34° C. At this site (no. 433, 32.2° C.) the water was quite basic, having a pH. of 8.8. Shallow, exposed, tropical lakes and ponds often reach a temperature as high as 25–30° C., so the conditions under which it was growing in Java need not be considered as totally different.

18. Oscillatoria Okeni Agardh

Flora 10, p. 633, 1827.

Plant mass dark blue-green. Trichomes straight, distinctly constricted at the cross walls, 5.5–9.0μ in diameter, gradually tapering toward the curved or somewhat hooked apex. Cells 0.3–0.6 diameter in length, 2.7–4.5μ long, with finely granular blue-green contents; cells near apex up to 8μ long; end cell rounded or almost pointed, neither capitate nor calyptrate.

Occurring in hot springs, cool standing water, warm salt water, sulphur springs, and brackish water, in North America, Europe, and Africa, *O. Okeni* is quite tolerant of variable conditions. It is probably cosmopolitan. Setchell and Gardner (1903) recorded it from brackish water in Washington. It is not well known in the United States.

Apparently rare in the Park, it has been noted only in the Stygian Caves, Mammoth Hot Springs (no. 150), at 15° C., pH. 7.7.

19. Oscillatoria Cortiana (Poll.) Menegh.

Consp. Alg. Eugan., p. 8, 1937.

Plant mass dark and often dull blue-green. Trichomes straight, fragile, slightly but distinctly constricted at the cross walls, gradually tapering toward

the curved and undulant apex, 5.5–8.0μ in diameter. Cells cir. 1 diameter in length, 5.4–8.2μ long; cell contents usually granular; cross walls not granulated; cells near apex elongate, up to 14μ in length; end cell blunt conical, rounded, neither capitate nor calyptrate.

Found in both cool and warm waters, it is widely distributed. In the United States it has been reported only from Pennsylvania (Wolle, 1877), floating on hot water from a factory.

It has been encountered in a single spring in the Park: Soda Spring, Mammoth Hot Springs region (no. 126), at 42° C., pH. 6.1. In this saline and atypic spring, *O. Cortiana* was present in large quantity.

20. OSCILLATORIA FORMOSA Bory

Dict. Class. d'Hist. 12, p. 474, 1827.

Plant mass dark blue-green. Trichomes 4–6μ in diameter, straight to flexuous, usually slightly constricted at the cross walls, apex slightly tapering and bent, end cell blunt-conical, acutely rounded, not capitate, without calyptra. Cells from one-half their diameter in length up to almost one diameter, 2.5–5.7μ long, cross walls often finely granulated, cell content bright blue-green.

O. formosa is a widely distributed species. It occurs not only over a wide area but includes many diverse habitats: standing water, pools, lakes, etc., brackish water, sewage-contaminated water, moist cliffs, sulphur springs, and thermal springs. It is known from North America, South America, Europe, Asia, and Africa, as well as several islands not belonging to any of the continental groups. In North America it has been found up to now only in non-thermal sources. These include the usual, variable assortment: still water, sewage-polluted streams, and brackish water.

In the Yellowstone I have found *O. formosa* as a regular component of the flora of certain springs. It is particularly prevalent in the cooler waters of shaded springs or rills in the Mammoth group. Its greatest abundance was noted in a pool in deep shade in the White Elephant Grottoes (no. 100) at a temperature of 33° C. and pH. 7.5. It was found in the overflow rills from the following springs: Jupiter Terrace and Blue Pools (near Mammoth Swimming Pool) (no. OS22), Cleopatra Terrace, and Main Terrace. It occurred in the spring pools of several small springs and seeps: in the Stygian Caves, White Elephant Grottoes, and in some exposed but small springs. Its range in temperature seems to be from about 40° C. down to strictly non-thermal conditions; its pH. tolerance is apparently wider than its Yellowstone distribution (pH. 6.4–7.8) indicates.

21A. Oscillatoria chalybea Mertens

var. depauperata, var. nov.

Plant mass bright blue-green, flocculent. Trichomes 5–8μ in diameter, long, straight to curved or irregularly and loosely spiraled, lightly constricted at the cross walls, very feebly narrowed toward the slightly bent tips, with blue-green cell contents. Cells 0.3–0.6 diameter in length, 1.7–4.0μ long; cross walls feebly or not granulated; end cells broadly rounded, up to 7μ long, neither capitate nor calyptrate.

Differing from *O. chalybea* chiefly in its smaller size, this variety is quite close to the species.

It has been found only in the Mammoth Hot Springs: Stygian Caves (type: no. 145), at 14° C., pH. 8.1, and in a runoff ditch below the spring terraces (no. Y2), at cir. 35° C. The plant is not common, and in a single collection only was in good quantity.

22. Oscillatoria Ulrichii Prát

Stud. biolith., Nák. České Ak., p. 97, 1929.

Plant mass indurated with lime, pale blue-green, dull olive-green to whitish; in culture (Prát) yellowish green to brownish. Trichomes straight to flexuously contorted, conspicuously constricted at the cross walls, 4.0–4.5μ in diameter, gradually tapering and curved at the apex. Cells 0.3–0.6 diameter in length, 1.5–3.0μ long, up to 12μ long at the apices; end cells broadly rounded to bluntly pointed, neither capitate nor calyptrate. Thin sheaths present in old strata.

This plant is extremely close to *O. Okeni* var. *fallax* Hansg. (*O. Okeni* var. *phormidioides* Hansg. seems unquestionably to be identical with the var. *fallax*.) *O. Ulrichii* may best be separated from *O. Okeni* var. *fallax* by its longer end cells and deeper constrictions at the cross walls.

Prát found the species in the Mammoth Hot Springs: near Jupiter Terrace, and in the White Elephant Grottoes, in cool and tepid waters.

In this investigation it was noted in several of the Mammoth Hot Springs: Jupiter Terrace, Angel Terrace, Hymen Terrace, Stygian Caves, and in others, at 14–34.6° C., pH. 7.2–8.05.

23. Oscillatoria geminata Menegh.

Comp. Alg. Eugan., p. 9, 1837.

Plant mass dull yellowish green. Trichomes rather fragile, irregularly contorted, often rolled, sometimes almost straight, distinctly constricted at the cross walls, 2.3–4.0μ in diameter. Cross walls thick, translucent. Cells 1–5 diameters in length, 2.3–16.0μ long; cross walls not granulated; cell contents

dull to clear blue-green, with mostly a few large refractile granules. Apices unspecialized; end cells rounded, neither capitate nor calyptrate.

Growing in standing water, on wet mud, in sulphur springs, brackish water and hot springs, *O. geminata* is probably cosmopolitan. It has been noted in non-thermal habitats in Minnesota (Tilden, 1898), and Washington (Setchell and Gardner, 1903). Tilden (1898) found it in the Yellowstone Park, in the swift current of a spring creek, at 47.5° C. The spring was near the Upper Geyser Basin.

It has been found in this study at Mammoth Hot Springs: Orange Spring Mound, Jr. (no. 82), at 43.6° C., pH. 7.65; Lower Geyser Basin: White Dome Geyser (no. 405), at 19.2° C., pH. 8.4; Upper Geyser Basin: Firehole River at spring below Giant Geyser, at 45.1° C., pH. 8.05; and in the Twin Buttes Region: Spray Geyser (no. 429), at 31° C., pH. 9.05. It is not common in the Park, but it is widely distributed.

23A. OSCILLATORIA GEMINATA Menegh.

var. fragilis, var. nov.

Trichomes straight, short, mostly 6–12-celled, 2.2–2.6μ in diameter. Cells 1–2 diameters in length, 2.3–5.1μ long. Otherwise as in the species.

This short-trichomed variety is much more common in the Park than *O. geminata,* and is quite distinct from it. The two forms were found together in one site and were very easily distinguished.

It has been noted in many springs including:—Mammoth Hot Springs: White Elephant Grottoes (type: no. 99), at 23.5° C., Stygian Caves (no. 148), at 13.1° C., pH. 8.2, ditch from Jupiter Terrace (nos. Y2, Y14), Angel Terrace overflow, Main Terrace; Meadow Springs (nos. 185, 187), at 55° C. and 48° C., pH. 6.6 and 6.65; Twin Buttes Region: Spray Geyser (no. 425), at 39.5° C., pH. 7.0, Imperial Geyser overflow (no. 419), at 31.3° C., pH. 8.95; Upper Geyser Basin: tepid pool; and Lower Geyser Basin: warm marsh near Firehole Lake. Its noted range included temperatures of 13.1° C. to 58.6° C., pH. 6.6 to 9.05.

23B. OSCILLATORIA GEMINATA Menegh.

var. tenella, var. nov.

Trichomes 1.7–2.0μ in diameter. Otherwise as in the species.

This slender variety was found consistently in the Stygian Caves, Mammoth Hot Springs, at cool temperatures and in deep to moderate shade. The type (no. 145) was at 14° C. and pH. 8.1. It was growing with *O. chalybea depauperata* (of this paper), *Gloeocapsa rupestris* Kütz., *G.*

arenaria (Hass.) Rab., *Gloeothece linearis* Naeg., and *Chroococcus minutus* (Kütz.) Naeg. The growth of the var. *tenella* was frequently abundant but it was not found in an unmixed stratum. The plant seems to be non-thermal, although in a situation kept moist by cooled thermal water.

24. Oscillatoria Jovis, sp. nov.

Filaments in clumps or scattered among other algae. Trichomes moniliform, short, fragile, mostly 30–60μ long but sometimes longer, straight to bent or curved, 3.4–4.2μ in diameter, very deeply and conspicuously constricted at the cross walls. Cells 3–5μ long, ovoid; cell contents blue-green; not granulated at the cross walls. Apices unspecialized, neither capitate nor calyptrate. Motility feeble.
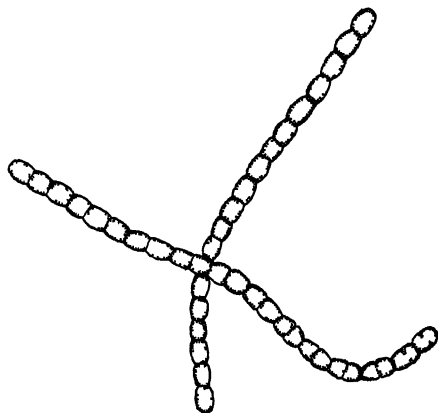
FIG. 57.—*Oscillatoria Jovis* (×690).

This aberrant *Oscillatoria* resembles *Pseudanabaena* in cell shape but does not have the separated cells that Lauterborn emphasized in the description of the genus. The cells, although shorter, are not unlike those of *P. tenuis* Koppe. It resembles no previously described species of *Oscillatoria* in other than generic characters.

This is probably the most widespread *Oscillatoria* in the Yellowstone, but is almost never abundant. In a single collection it was the dominant alga. It has been noted in the following springs:—Mammoth Hot Springs: Orange Spring Mound, Orange Spring Mound, Jr. (nos. 77, 78, 79, 80, 81, 82, 86) (type: no. 80, 51.6° C., pH. 7.0), White Elephant Grottoes (nos. 97, 101), Angel Terrace (no. 155), Jupiter Terrace, Diana Terrace, Narrow Gauge Terrace, Mound Terrace, Cleopatra Terrace; Meadow Springs (no. 193); Lower Geyser Basin: seven springs; Upper

Geyser Basin: Handkerchief Pool (nos. 350, 351) and eleven other springs; West Thumb: five springs; Elk Park: unnamed spring (no. 210); Twin Buttes Region: Spray Geyser (nos. 424, 428); and elsewhere. It was not noted in the Norris Geyser Basin, Mud Volcanos, or other extremely acid springs. It grew in water varying from 31° to 71.° C., pH. 6.45 to 8.95; its optima appeared to be near 50° C., pH. 7.6.

ARTHROSPIRA Stizenberger

Hedwigia 1, p. 32, 1852.

Filaments solitary or united into mostly slimy blue-green, olivaceous, or reddish brown strata. Trichomes cylindrical, regularly or rarely somewhat irregularly twisted into definite spiral coils, long or rarely few-celled and short. Sheaths absent. Cross walls visible without staining, and visible in living specimens.

Type species: *Arthrospira Jenneri* Stizenberger.

Separated from *Spirulina* Turpin chiefly by the visible cross walls, many authors have preferred to unite the two genera. The disposition of this matter is of little consequence. The species of *Arthrospira* are larger than those of *Spirulina*.

The various species inhabit most frequently standing or flowing fresh water, less often brackish or salt water. They often occur on or among other algae. A single species, *A. maxima* Setchell & Gardner, has been reported from warm (salt) water at Oakland, California (Gardner, 1917). There are no previous records of the genus from the Yellowstone.

A single Yellowstone species.

1. ARTHROSPIRA JENNERI Stizenberger

Hedwigia 1, p. 32, 1852.

Filaments single or united into a blue-green mass. Trichomes blue-green, feebly or not at all constricted at the cross walls; 5–8μ in diameter; with rounded, unspecialized apices; mostly regularly spirally coiled. Coils 9–15μ in diameter; 21–31μ between adjacent turns. Cells quadrate or shorter than their diameter, 3–6μ in length; mostly finely granulated at the cross walls; end cells broadly rounded.

This cosmopolitan fresh-water alga has been found in many localities in the United States, growing in standing or flowing water, among other algae or alone, submerged or floating.

In the Yellowstone it has been noted twice in the present study, both times in non-thermal water. It was found in Panther Creek, growing among *Batrachospermum;* and in the Gardiner River below Boiling

River, mixed with various algae, at 18.6° C. The water at the latter site was feebly warmed by thermal springs.

SPIRULINA Turpin

Dict. d'hist. nat. de Levrault, p. 50, 1829.

Trichomes regularly spirally twisted into a more or less regular coil, without sheaths. Cross walls absent or invisible without special staining. Trichomes long to short; coils tight to lax. Trichome apices unspecialized. Cell walls rigid, not flexible; motility often marked but of the *Oscillatoria* type.

The several species live in fresh, brackish, salt, sulphide-containing, and warm waters; terrestrial habitats are not favored. Of the known thermal species: *S. caldaria* Tilden, *S. maior* Kütz., *S. subsalsa* Oersted, *S. Meneghiniana* Zanard., and *S. labyrinthiformis* Gom., two have been reported from hot springs in North America. *S. caldaria* was described from hot sulphur springs at Banff, Alberta, Canada, by Tilden (1898), and *S. maior* reported from the Yellowstone by Tilden (1898).

In the Park one species is quite important, and others are not uncommon.

KEY TO THE YELLOWSTONE SPECIES.

I. Turns of the trichome separated, not in contact.
  1. Coils open, lax.
    A. Coils cir. 1.5μ in diameter.   *S. caldaria* 1.
    B. Coils cir. 3.0μ in diameter.   *S. caldaria* var. *magnifica* 1A.
  2. Coils moderately close.
    A. Trichomes cir. 0.4μ in diameter.   *S. tenerrima* 2.
    B. Trichomes 0.6μ or more in diameter.
      a. Trichomes 0.6–0.9μ in diameter.   *S. subtilissima* 3.
      b. Trichomes 1.2–1.7μ in diameter.   *S. maior* 4.
II. Turns of the trichome in contact.   *S. labyrinthiformis* 5.

1. SPIRULINA CALDARIA Tilden

Bot. Gaz. 25, p. 103, 1898.

Trichomes short, somewhat straight and stiff, cir. 0.9μ in diameter and up to 15 or 20μ in length, forming a lax spiral 1.5μ in diameter, cir. 3.2μ between the turns. Plant mass extended, dark blue-green; or filaments scattered among other algae.

The type locality for the plant is the Natural Sulphur Springs, Banff, Canada, where in 1897 Tilden found the plant forming richly colored strata on the surface of hot water (how hot?). There are no other records for the plant.

In the Yellowstone *S. caldaria* is of rare occurrence and has been observed only when mixed with other algae: *S. labyrinthiformis* Menegh, *Oscillatoria terebriformis* (Ag.) Gom., and *Phormidium laminosum* (Ag.) Gom. I have found the plant only in the Mammoth Hot Springs: White Elephant Grottoes (no. 100), at 33° C., pII. 7.5, and Orange Spring Mound, Jr. (no. 84), at 30.2° C., pH. 8.0. From the data available it favors a moderate temperature, persisting in cultures at room temperature, and disappearing at temperatures of above 45° C.

1A. SPIRULINA CALDARIA Tilden

var. **magnifica**, var. nov.

Trichomes short, straight or flexuous, 0.7–1.0μ in diameter and up to 40 or 50μ in length, forming a lax spiral cir. 3μ in diameter and 8–10μ between the turns. Cell contents pale blue-green, homogeneous. Filaments solitary or in flocculent flakes; mass olivaceous blue-green and very soft.

FIG. 58.—*Spirulina caldaria var. magnifica* (×1860).

The larger, looser, less rigid coils separate the variety from *S. caldaria*. The motility of the filaments is notable.

It is wide spread and frequent in the Yellowstone. The type (no. 80) is from Orange Spring Mound, Jr., Mammoth Hot Springs, 51.6° C., pH. 7.05. It has been noted in the following sites:—Mammoth: Orange Spring Mound, Orange Spring Mound, Jr. (nos. 79, 80, 81, 82, 83, 84, 85, 86, 87), Jupiter Terrace, Main Terrace, Narrow Gauge Terrace, Diana Terrace, Hymen Terrace, Cleopatra Terrace, Blue Pools overflow, and White Elephant Grottoes (nos. 89, 99, 101) ; Meadow Springs (no. 187) ; Boiling River group: Riverside Cone (no. 272) ; Elk Park: small spring (no. 210) ; Upper Geyser Basin: Bijou Geyser (nos. 440, 441, 442) and eleven other springs; Biscuit Basin: Jewell Geyser (no. 374) ; Lower Geyser Basin: seven springs; and in a few scattered springs. It has not been noted in the Norris Geyser Basin, or in the Mud Volcano Group. It has been observed at temperatures of from 16.9° C. to 57° C., at acidities of pH. 6.55 to 9.0. Below 35° C. it was invariably quite rare and its growth seemed best at cir. 45° C.

2. SPIRULINA TENERRIMA Kützing

Phyc. gen., p. 183, 1843.

Trichomes 0.4μ in diameter, regularly spirally twisted into a uniform coil 1.4–1.7μ in diameter, clear blue-green; distance between the turns 1.0μ; distance between adjacent portions of contiguous coils of trichome approximately 0.4μ.

S. tenerrima occurs chiefly on damp earth among other algae, especially species of *Oscillatoria* and of *Phormidium*. The only record of this species from North America is by Farlow. He gave no locality reference.

The presence of this species in a hot spring, or in thermal habitats, is unexpected. I have found it among other algae in a small warm pool between Oblong Geyser and Giant Geyser in the Upper Geyser Basin (no. 445), growing submerged in water at a temperature of 34.9° C. and pH. 8.55. It is not an important component of this, or as far as I am aware, of any other hot spring. There are no other records of the species from warm water, and very few from submerged situations.

3. SPIRULINA SUBTILISSIMA Kützing

Phyc. gen., p. 183, 1843.

Plant mass dark green, slimy. Trichomes 0.6–0.9μ in diameter, regularly spirally twisted, pale to bright blue-green, rarely yellowish. Coils 1.5–2.8μ in diameter; adjacent turns 1.2–2.0μ apart; contiguous portions of adjacent coils cir. 1μ apart.

This species is widely distributed and inhabits a notable range of situations: quiet fresh water, polluted water, brackish, and salt water, sulphur springs and hot springs. In the United States it has been reported from Nebraska and California.

Its occurrence in the Yellowstone is of interest in comprising one of the very few records of it in distinctly thermal waters. It has been found in the Firehole River, Upper Geyser Basin, at the point of entrance of a hot spring overflow, at 32.2° C. and pH. 8.8 (no. 443). It was present in small quantities mixed with *Oscillatoria* spp. and *Anabaena variabilis* Kütz.

4. SPIRULINA MAIOR Kützing

Phyc. gen., p. 183, 1843.

Stratum dark blue-green. Trichomes 1.2–1.7μ in diameter, regularly spirally twisted in a coil 2.5–4.0μ in diameter, 2.7–5.0μ between adjacent turns, cir. 1μ between adjacent portions of contiguous coils; pale or bright blue-green.

S. maior is a common and cosmopolitan alga of fresh, brackish, and warm waters. It is found mostly mixed with other algae. In the United States it has been reported chiefly from western states, although it occurs abundantly in the east. The alga has been reported from thermal waters in the United States three times. Tilden (1897) found it in hot (?) water at Bick's Hot Spring in Salt Lake City, Utah. Butler and Polley collected it in a warm sulphur spring at Banff, Canada. Tilden (1898) reported it from the Yellowstone, stating that "This species is quite common in both the calcareous and siliceous waters of Yellowstone Park. It is generally found with other algae." Her localities included Upper Geyser Basin: Spasmodic Geyser, 49.0–54.5° C.; and Mammoth Hot Springs (no definite citation), 41° C.

I have been able to confirm the presence of *S. maior* in the Park, but I have found it chiefly in the Geyser Basins:—Upper Basin: Bijou Geyser (no. 438), 37° C., pH. 8.95, Emerald Spring, Chromatic Spring, and White Pyramid Geyser Cone (in seep); Lower Basin: two springs. At Mammoth it has been noted only once, in Orange Spring Mound, Jr. (no. 84), at 30.2° C., pH. 8.0. In all of these springs the plant was rare. *S. maior* is not "quite common in both calcareous and siliceous waters"; it is rare to very rare in most of the springs. It is probable that Tilden confused the completely distinct *S. labyrinthiformis* with *S. maior*. Her temperature records are of no validity because of the probable misidentification. The plant has been noted at from 26° C. to 43.7° C., in basic waters, pH. 7.7–8.95.

5. SPIRULINA LABYRINTHIFORMIS Gomont

Monogr. Oscill., p. 275, 1893.

Trichomes often very long, cir. 1μ in diameter, blue-green, very regularly twisted; forming a smooth shining brilliant green to dull blackish green stratum. Coils tight, the adjacent turns in contact, 2.0–2.7μ in diameter.

Occurring in standing brackish water and in hot springs in Europe and Africa, the species has been unknown in America up to the present.

In the Yellowstone it is widespread and extremely abundant, and is unquestionably the most important species of its genus. It is the only *Spirulina* I have encountered in the Park in pure strata. It is possible that Tilden's records of *S. maior* Kütz. are in error and should refer to this species. She stated of *S. maior* (1910), "This species is quite common in both calcareous and siliceous waters of Yellowstone Park." Her statement is true of *S. labyrinthiformis* and certainly is not true of *S. maior*. In the present study it has been noted in the Mammoth Hot

Springs: Orange Spring Mound, Orange Spring Mound, Jr. (nos. 78, 79, 80, 81, 82, 83, 86, 87), White Elephant Spring, White Elephant Grottoes (nos. 89, 90, 94, 97, 98, 99), Angel Terrace, Jupiter Terrace, Narrow Gauge Terrace, Diana Terrace, Minerva Terrace, Main Terrace, Blue Springs, and others; Upper Geyser Basin: Bijou Geyser (no. 438), Punch Bowl Spring, Wave Pool, Chromatic Pool, Emerald Spring, Morning Glory Spring overflow, and others; Lower Geyser Basin: seventeen springs; Twin Buttes Region: Spray Geyser (no. 430), Imperial Creek; Soda Spring (Mammoth Region); West Thumb: five springs; Shoshone Geyser Basin: two springs; and in several isolated springs. It seems to be absent from the Norris Geyser Basin, Mud Volcano Springs, and the Crater Hills. It ranged in distribution from 23° C. to 59.4° C., from pH. 6.05 to 8.05, with its greatest abundance at cir. 44° C. and pH. 6.7. Between the temperatures of 30° and 50° C. it could be found in every sample at Mammoth, and in the less sharply acid and basic springs elsewhere.

GLAUCOSPIRA Lagerheim

Ber. deutsch. bot. Ges. 10, p. 364, 1892.

Filaments regularly spirally twisted, long, slender, without sheaths. Cell walls thin, flexible; cross walls absent or invisible. Motility Spirochaete-like. Flagella and undulating membrane absent. Pigments present including chlorophyll and phycocyanin.

Type species: *Glaucospira agilissima* Lagerheim.

The similarity of *Glaucospira* to *Spirulina* Turpin is notable. However, the flexible cell membrane is unique among the Myxophyceae, and the rapid peculiar motility is completely distinctive. The rigid filaments of *Spirulina* that at most bend slowly without aiding in forward movement contrast with the flexible, serpentine, writhing filaments of *Glaucospira*. The species described below is fully as active as the species of *Leptospira* and certain other Spirochaetes the author has observed and it seems probable that the relationships of *Glaucospira* lie in this direction rather than with the Myxophyceae.

The two very similar previously described species, *G. agilissima* Lag. and *G. tenuior* Lag., are known only from Quito, Ecuador.

A single Yellowstone species.

1. Glaucospira yellowstonensis, sp. nov.

Trichomes regularly coiled, cir. 0.5μ in diameter; coils up to 40μ in length, 3-5μ in diameter, distance between adjacent turns 3-6μ. Cell contents bright blue-green, homogeneous. Motility very rapid; trichomes flexible.

The species of Lagerheim have a trichome diameter of 2µ and somewhat less. The much more slender trichomes of this species are distinct. While alive, the movement is too rapid to permit accurate measurement of the organism. However, the coil diameter, distance between turns, and over-all length are changed materially as the trichomes move. In *Spirulina*, if such changes occur, they are of extremely minute proportions. The measurements above are from fixed specimens and do not present the extremes to be observed in living material. The trichome diameter is, of course, constant.

This unique species has been found as an incidental species in Firehole Lake, Lower Geyser Basin (no. 400, type), at 28–37° C., pH. 8.3. It was present on the surface of the chocolate-brown gelatinous bottom crust of the lake. This crust consisted of *Phormidium laminosum* (Ag.) Gom., *Lyngbya subspiroides* (of this paper), and incidental species such as *Aphanothece saxicola* Naeg., *Synechococcus Minervae* var. *maior* (of this paper), and *Spirulina caldaria* Tilden. It was possible to obtain almost pure flecks of the *Glaucospira*. The masses of filaments were bright blue-green, flocculent, and easily broken up. The reaction of the organism to light was sharply positive.

PHORMIDIUM Kützing

Phyc. gen., p. 190, 1843.

Filaments unbranched, straight or contorted but never regularly spirally twisted; united into gelatinous, slimy, cartilaginous, membranaceous, felted, or leathery strata attached broadly to the substratum or forming partially free, rarely floating, corded masses, or more or less columnar, sometimes bulbous thalli. Sheaths more or less firm, thin, and uniform, gelatinized, slightly to completely confluent, and sometimes forming a homogeneous matrix. Trichomes mostly long. Hormogonia present. Resting cells absent.

The large number of species belonging to this especially difficult genus grow almost everywhere; standing and flowing fresh water, brackish, salt, and supersaline waters, polluted water and mineral springs, sulphur springs and thermal waters, damp soil, rocks, and mud, even caves, all have species of *Phormidium* as regular components of their algal flora. The genus is especially well represented in hot springs, and at least twenty-six species have been noted in the past in thermal habitats. Five have been reported from the Yellowstone, and in this investigation twenty-one species and varieties have been found, giving a total of twenty-two Yellowstone thermal species of *Phormidium*. The Yellowstone forms will be considered individually. Of the ones not found in the Park, the following have been credited to thermal springs: *P. Treleasii* Gom., *P.*

africanum Lemm., *P. purpurascens* var. *homogeneum* Gardner, *P. gela-
tinosum* Woron., *P. orientale* G. S. West, *P. valderianum* var. *tenuis*
Woron., *P. ambiguum* Gom., *P. Corium* Gom., *P. papyraceum* Gom., *P.
viscosum* Lemm., *P. calidum* (K. B. H.) Gom., *P. lucidum* Kütz., *P.
uncinatum* Gom., *P. Chungii* Gardner, *P. inundatum* var. *conspersum*
Menegh., and *P. favosum* (Bory) Gom. Only a few of these are known
in thermal waters from North America. *P. purpurascens* var. *homo-
geneum* was described from a hot spring in Porto Rico (Gardner, 1927),
and *P. Treleasii* is known from warm waters in Arkansas (Gomont, 1899)
and a hot sulphur spring at Banff, Alberta (Gardner and Setchell, 1903).
Certain species of the genus live at very high temperatures. Gardner
(1927) found *P. Chungii* at 70° C. in a spring in China, and Tilden
(1898) reported *P. laminosum* (Ag.) Gom. from the Yellowstone, where
she found it at 75.5° C.

In the Park, *Phormidium* is unquestionably the most important genus
of thermal algae. The genus is represented in all of the springs except
those of extreme acidity, and those that due to turbidity of the water or
violence of eruption house no living organisms. In some springs, e.g.
Spray Geyser, the strata of *Phormidium* reach a thickness of 10 cm. In
many cases the mixed strata of some of the smaller species present almost
hopeless taxonomic problems. The majority of the springs have very
definite *Phormidium* formations as the dominant associations at tempera-
tures of 40° to 75° C. Several of the species are typically thermal. It is
notable that the Yellowstone forms include mostly the smaller species,
and of the twenty-two known in the Park only a single one has a trichome
diameter as great as 4μ. A few of the species are considerably less than
1μ in diameter. Two of the species are typical thermal limital types,
extending their range up to the highest temperatures endured by living
organisms. The temperature of 85.2° C. permits the slow growth of at
least one species, *P. bijahensis* (of this paper), and a second grows at a
temperature of 84° C. Two other species extend into water above 70° C.

<div align="center">KEY TO THE YELLOWSTONE SPECIES.</div>

I. Trichomes greater than 5μ in diameter.*   *P. yellowstonense* 1.
II. Trichomes less than 4μ in diameter.
  1. Trichomes greater than 0.7μ in diameter.
    A. End-cells or trichome apices or both tapering.
      a. End-cells pointed; trichome apices not otherwise tapering; not
         constricted at cross walls.
        *. Cells longer than broad.
          !. Trichomes 1.0–2.0μ in diameter; end-cells not hooked.
                                 P. laminosum 2.

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* *Mastigocladus laminosus* var. *phormidioides* might be sought here.

!!. Trichomes 2.6–3.2μ in diameter; end-cells often hooked.

                P. vesiculosum 4.

**. Cells isodiametric or shorter than broad.   *P. Weedii* 3.

b. Trichome apices tapering; constricted at cross walls.

 *. Calyptra present.   *P. subcapitatum* 5.

 **. Calyptra absent; end-membrane unthickened.

  Cells short, 0.6–1.3 diameters in length.   *P. fragile.* 6.

  Cells longer, 1.4–5.5 diameters in length.

   ‡. Trichome diameter 2μ or greater. *P. subuliforme* 7.

   ‡‡. Trichome diameter 2μ or less.

    x. Cross walls without granules; cells up to 3 diameters in length.   *P. tenue* 8.

    xx. Cross walls mostly with two granules; cells up to 5.5 diameters in length.

         P. tenue var. *granuliferum* 8A.

B. End-cells not pointed; apices not tapering.

 a. Trichomes constricted at the cross walls.

  *. Trichomes deeply and prominently constricted; trichomes moniliform.   *P. foveolarum* 9.

  **. Trichomes lightly and inconspicuously constricted.

   !. Stratum dark violet, steel blue, or blue-black.

             P. luridum 10.

   !!. Stratum bluish to yellowish green.

    ‡. Trichomes 2.0–2.5μ in diameter; stratum lamellate.

           P. valderianum 11.

    ‡‡. Trichomes 1.3–2.0μ in diameter; stratum not lamellate.

     P. valderianum var. *cartilagineum* 11A.

 b. Trichomes not constricted at the cross walls.

  *. End-cells blunt, truncate, or subtruncate.

       P. truncatum var. *thermale* 12A.

  **. End-cells rounded, neither truncate nor flattened.

   !. Cells 0.6–1.2 diameters in length; stratum red.

             P. rubrum 13.

   !!. Cells 1.0–4.0 diameters in length; stratum not red.

    ‡. Stratum purplish to violet brown.

     x. Cells 1–2 diameters in length; trichomes 1.5–2.5μ in diameter. *P. purpurascens* 14.

     xx. Cells 2–4 diameters in length; trichomes 1.0–1.4μ in diameter. *P. purpurascens* var. *laminatum* 14A.

    ‡‡. Stratum blue-green or bluish to yellowish green.

     x. End-membranes thickened; stratum with long free tufts, fibrous.   *P. ramosum* 15.

     xx. End-membranes unthickened; stratum smooth, spongy, gelatinous. *P. acidophilum* 16.

2. Trichomes less than 0.7μ in diameter.

 A. Stratum fibrous, tufted, and with corded streamers.

           P. geysericola 17.

 B. Stratum not fibrous, plane.

  a. Stratum yellow-green, leathery.   *P. subterraneum* 18.

  b. Stratum pink to red, soft spongy.   *P. bijahensis* 19.

1. PHORMIDIUM YELLOWSTONENSE Prát

Stud. biolith., Nák. České Ak., p. 97, 1929.

Stratum extended, indurated with lime. Filaments more or less parallel, straight or irregularly spirally twisted. Sheaths at first thin, later firm and evident, incompletely confluent. Trichomes blue-green, not constricted at the cross walls, 6–8μ in diameter; apices straight and more or less attenuate, feebly capitate and sometimes twisted. Cells mostly 0.5–1.0 diameters long (occasionally as short as 1/4 diam.) ; end cells rounded at apex or subconical, with distinct calyptra.

This plant was found by Prát in the reservoir at Mammoth, growing mixed with *Calothrix*. The water in the reservoir is cool, but is partly of thermal origin. The species is to be expected in the cooler waters of the nearby springs.

It was not encountered in this investigation.

2. PHORMIDIUM LAMINOSUM (Ag.) Gomont

Essai Class. Nost. homocyst., Morot. Jour. Bot. 4, p. 355, 1890.

Stratum thin or less often thick, up to 1 cm., membranous to grisly, bright blue-green, golden, or reddish. Filaments flexuous to contorted, entangled. Sheaths colorless, close, of variable thickness, often papery, usually completely or almost completely confluent into an amorphous matrix. Trichomes 1.0–2.0μ in diameter (usually near 1.5μ), not constricted at the cross walls; apices straight, cylindrical except for the apical cell. Cells longer than broad, 2–5μ in length, mostly with 2–4 refringent granules on the often inconspicuous cross walls; cell contents pale blue-green. End-cells sharp pointed, without calyptra.

This widespread species occurs in standing water, on wet rocks, and in hot springs. It is known from almost every major hot spring group and from numerous non-thermal sources. In North America it is known from Alaska (Saunders) to Trinidad (Howard) ; and from a variety of habitats: waterfalls, quiet pools, greenhouses, and warm springs. Kellerman in 1906 (Tilden, 1908) found it in very warm (?) water near Lake Amatitlan, Guatemala.

Tilden found the plant in 1896 (1898) in various hot springs in the Yellowstone: Norris Geyser Basin: Ribbon Spring; Lower Geyser Basin: Mountain Hot Springs and springs in the Nez Perces valley; Upper Geyser Basin: Solitary Spring; Midway Geyser Basin: Grand Prismatic Spring; and Mammoth Hot Springs (which ones?) ; at temperatures ranging from 30° C. to 75.5° C. About the species she stated that it was found to be "by far the most widespread and abundant of any in the

hot waters of the park. Its habit of growth is extremely varied, so that it is not easily recognized. It is the only species, except *Spirulina major,* that, so far as I know, is found in both calcareous and siliceous waters in this region." From my own experience, I am in agreement with Tilden in her statement concerning the abundance, widespread occurrence, and
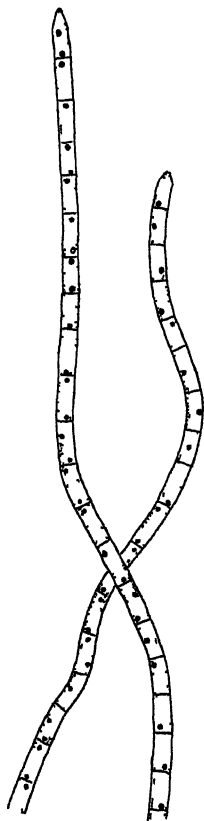

FIG 59 —*Phoi midium la- minosum*   (Ag)   Gom (×1650).

variable appearance of *P. laminosum.* It is present regularly in most of the larger and many of the smaller hot springs in the Park, within certain limits of temperature and acidity. In my collecting I have found it in the following springs:—West Thumb : eight springs ; Upper Geyser Basin : Handkerchief Pool, Emerald Pool, Rainbow Spring, Bijou Geyser, Beach Spring, Wave Spring, Cyclops Springs, Giantess Spring, and others ; Mid-

way Geyser Basin: Grand Prismatic Spring, Turquoise Pool, Excelsior Geyser Crater, Iris Pools, and several small unnamed springs; Lower Geyser Basin: Ojo Caliente Spring, Black Warrior Springs, Surprise Pool, Five Sisters Springs, and others; Twin Buttes Region: Spray Geyser, Imperial Geyser, and two small springs; Norris Geyser Basin: rare or absent; Mammoth Hot Springs: Orange Spring Mound, Orange Spring Mound, Jr., Minerva Terrace, Angel Terrace, Jupiter Terrace, Diana Terrace, White Elephant Spring, and several others; and in many isolated springs. I suspect that in Tilden's work there was some confusion between *P. laminosum* and other small species of *Phormidium*. This is suggested by her description of the plant growth, including as she does, extremely variable and aberrant types: pink, yellow, white, and green masses; white scurfy brittle scum on surface of pools; foliated and bulbous to ribbon-like and plume-like growth, as well as the usual types of strata. In my own experience, the species varies widely in appearance, but within limits, forming always distinctly colored masses, blue-green, yellowish-brown, orange-tan, and grading into a yellowish brick-red. The color range is evidently correlated with the plant's ability to effect a certain degree of chromatic adaptation. The orange-tan and brownish strata are usually in full sunlight and well exposed, the blue-green strata are partially shaded, and the reddish types occur beneath the surface or in deep shade. The Yellowstone material is undoubtedly that indicated by Boresch as var. *olivaceo-fuscum*. I consider his variety to be the *P. laminosum* (Ag.) of Gomont, and the varietal name unnecessary. *P. laminosum* seems to occur at temperatures up to 65–66° C. and not above (Tilden's record of 75.5° C. is too high), and at acidities of pH. 6.0 to 9.0. In colonial morphology the alga is quite constant under uniform conditions. In very shallow rills and pools it may form thick cartilaginous to leathery, partially submerged rims or "islands"; in deeper, quiet water it forms softer strata, usually smooth but often with raised ridges, papillae, or erect columnar processes (the processes become bulbous above chiefly when they reach the surface of the water and develop into small islands); in swift water it forms streamers and elongate ridges. Its appearance is often modified by the growth of epiphytic species, and by mixture with other species of *Phormidium*, with *Mastigocladus*, etc.

In many springs *P. laminosum* is the dominant alga over extended areas. It has given the name to Orange Mound, on which it is abundant and where its orange-tan strata are quite handsome.

3. Phormidium Weedii (Tilden) comb. nov.

Syn.: *Phormidium laminosum* (Ag.) Gom. forma *Weedii* Tilden,
Bot. Gaz. 25, p. 99, 1898.

Stratum blue-green. Trichome more or less contorted, and irregularly crowded, not constricted at the cross walls. Sheaths difficultly visible, thin, mostly confluent into a general matrix. Trichomes 2.5–3.0μ in diameter; apices pointed. Cells 0.5–1.0 diameter in length, 1.5–2.5μ long, cross walls mostly without granules; cell contents blue-green, usually granular. End-cells sharp conical, neither capitate nor calyptrate. Apices neither tapering nor bent or curved, but trichomes mostly bent to hooked a short distance behind the apex.

Tilden stated that "the apex is almost invariably sharply bent." The bend is not especially constant, although it is typical, and the bends occur indiscriminately at any point behind the apex. I find the plant to be constantly distinct from *P. laminosum,* and as distinct as the majority of species of the genus. It is, as Tilden noted, similar to *P. laminosum.* The cell length is particularly distinctive, and the shorter, broader cells separate it from that species. The alga was described from the Yellowstone, and was found (by Weed) in the overflow channel of Spasmodic Geyser, Upper Geyser Basin, at 49–$54.3°$ C.

It has been noted in five springs in the Upper Geyser Basin: Sunset Lake, Beauty Pool, Lion Geyser overflow, Wave Spring, and Goggles Spring, at 37.8–$59.9°$ C., pH. 8.2–9.05; and in Spray Geyser, Twin Buttes Region (no. 417), at $47.2°$ C., pH. 8.9. In general it is of secondary importance in the springs in which it was studied.

4. Phormidium vesiculosum, sp nov

Stratum gelatinous, homogeneous, translucent and pale blue-green to golden-green, up to 1 cm thick, frequently and characteristically with long or short, flexible, gelatinous, erect or waving cords arising from the upper surface, 3–10 mm. in diameter and up to 0.6 m long, bearing at their upper ends gas-filled sacs or vesicles 1–6 cm. in diameter, that tend to float at the surface and support the cords in an erect position. Trichomes not crowded, straight to flexuous, not contorted, often more or less parallel, alike in all parts of the plant mass, 2.6–3.2μ in diameter (usually 3.0μ), often very slightly constricted at the cross walls. Sheaths invisible, completely confluent into a colorless, homogeneous matrix. Cells cylindrical, 6–15μ in length (usually 8–12μ), much longer than their diameter, frequently spaced in the trichome with the gap between cells up to 0.5μ, pale blue-green, with usually two polar granules which lie at or near the end walls. Apices straight, not tapering (except for the end-cells). End-cells at first rounded, then obtusely pointed, gradually becoming long, sharp-pointed, and sometimes with a tiny bent hook on the tip, without calyptra; terminal half or two-thirds of each end cell modified, remainder of cell normal.

P. vesiculosum is quite distinct from all other species of *Phormidium*. It is closer to *P. laminosum* (Ag.) Gom. and *P. Weedii* (Tilden) than to
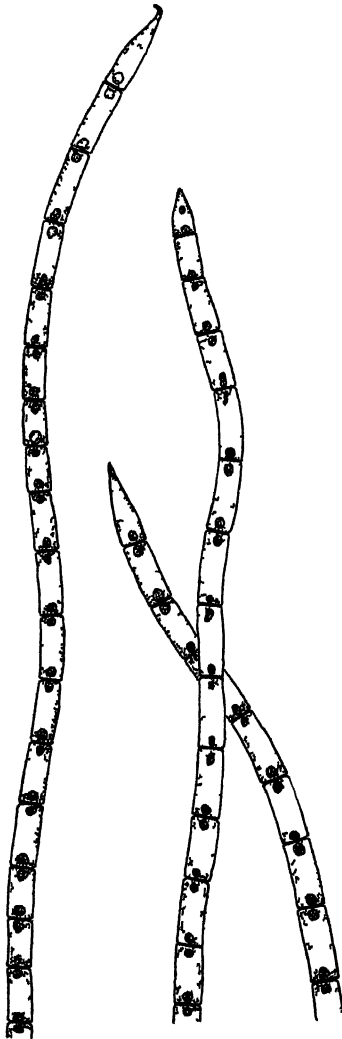
Fig 60 —*Phormidium   vesiculo-
sum* (×1200)

other species. From them it may be distinguished by its larger trichomes, its peculiarly hooked end-cells, its rather more homogeneous stratum, and its distinctive bladder-bearing cords.

It is of considerable interest that the cords form best in quiet water, and have a constant morphology. The length of the cord is usually, at maturity, just the depth of the water. In shallow basins the strata bear sessile blister-like vesicles or very short stalked ones. The species is, to me, one of the handsomest of the Myxophyceae, and a hot spring pool literally filled with dozens of golden-green or pale blue-green translucent stalked balloons is a sight that one does not soon forget.

The plant is local and rather uncommon. It has been collected in only five springs: Main and Blue Pool Terraces, Mammoth; Bijou Geyser, Upper Geyser Basin (nos. 350, 351); and a small spring in the northeast part of Elk Park (type: no. 210). The alga occurred at 40–58° C., at pH. 7.5–9.0. The type was at 47° C. and pH. 8.05. It seems odd that so conspicuous a plant had not been described by previous workers in the Park.

5. PHORMIDIUM SUBCAPITATUM Boye Pet.

Freshw. Cyanoph. Iceland, p. 282, 1923.

Stratum membranous to leathery, dark blue-green. Sheaths slimy, mostly indistinct. Trichomes irregularly twisted, 1.8–2.2μ in diameter, lightly constricted at the cross walls; apices straight, often slightly narrowed. Cells 1–2 diameters in length, 2–6μ long; end cells often feebly capitate, with rounded or blunt conical calyptra.

Up to the present it has been reported only from Iceland, where it grew on damp earth.

In the Yellowstone it was noted once, on the cone of Bijou Geyser in the Upper Geyser Basin (nos. 436, 437). At the time of collection it was at 42° C., pH. 8.95. The temperature at the site at which it grew varied from 26 to 53° C. during a few hours time. The acidity remained constant. With these meager data it is not possible to place the alga ecologically.

6. PHORMIDIUM FRAGILE (Menegh.) Gom.

Monogr. Oscill., p. 163, 1892.

Stratum slimy-gelatinous, often lamellate, yellowish to brownish blue-green. Sheaths confluent, difficultly visible. Trichomes flexuous, twisted and interwoven or more or less parallel, distinctly constricted at the cross walls, gradually tapering at the apex, 1.2–2.3μ in diameter, pale blue-green. Cells mostly almost isodiametric, 1.2–3.0μ long, not granulated at the cross walls; cell contents homogeneous. End cells pointed, conical, neither capitate nor calyptrate.

Growing in salt, brackish, and fresh water, in sulphur and warm springs, *P. fragile* is cosmopolitan. It has been noted several times in the United States, but has not been recorded from either the Yellowstone Park or hot waters.

It is rare in the Park, and has been found only in the Stygian Caves, Mammoth Hot Spring, (no. 146), at 12.8–23.1° C., pH. 7.9–8.1.   It was present on the wet walls of the shallow shaded grotto in profusion.
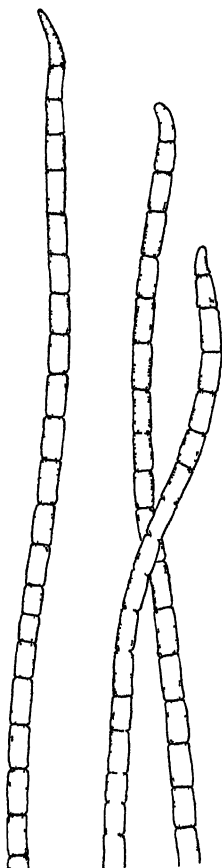
FIG. 61.—*Phormidium sub-uliforme* Gom. (×1000).

7. PHORMIDIUM SUBULIFORME Gom.

Monogr. Oscill., p. 189, 1892.

Stratum lamellate, yellowish-green to olive-green.   Filaments mostly parallel, straight or flexuous.   Trichomes 2.0–2.8μ in diameter, lightly constricted at the cross walls, dull blue-green, cross walls often inconspicuous; at the apices tapering and bent or twisted, not capitate.   Sheaths completely confluent into a homogeneous matrix.   Cells up to 4 times their diameter in length, 3.4–8.0μ long, with homogeneous (or coarsely granular?) contents. End-cell usually acute-conical with acutely rounded tip, calyptra none.

In the Yellowstone material the uniformly homogeneous cell contents is notable. This is in agreement with Gomont's original diagnosis and in partial disagreement with Tilden (1910). The color of the stratum is variable—not the constant golden-green of previous records—ranging from dull tan, golden-green to olive-green and dull blue-green. Geitler (1925, 1932) questioned the invariably constant color.

P. subuliforme has been found very few times. Geitler (1925) states that it has been collected only four times. These records established the species in St. Paul, Iceland, and Algeria—in hot springs in each case. Bessey, Pound, and Clements (1901) recorded its presence in an aquarium at Lincoln, Nebraska. It seems quite possible that their identification was in error. At any rate, its presence in such a situation is unexpected. In Yellowstone National Park the plant is local and not abundant. It has been noted chiefly in shaded sites, in the major Geyser Basins and at Mammoth. Its known range in the Park includes:—Upper Basin, the damp sides of a "cave" formed by the overhanging sinter ledge on the bank of the Firehole River between Oblong and Giant Geysers (no. 446), growing at 25° C.; Lower Basin, along the edge of a shaded thermal rill near Ojo Caliente Spring, growing at 32° C.; and Mammoth Hot Springs, generally found as an occasional to frequent component of the flora of the majority of springs (nos. 82, 83), growing below the surface of the algal strata and not forming a definite thallus. On the basis of the meager data available it seems that the species usually is favored by a moderate temperature (25° to 43.6° C.), slightly to moderately basic waters (pH. 7.65 to 8.2), and light of less intensity than that of full sunlight.

8. PHORMIDIUM TENUE (Menegh.) Gomont

Monogr. Oscill., p. 169, 1892.

Stratum membranaceous, extended, blue-green. Trichomes straight or somewhat entangled, more or less parallel, lightly constricted at the cross walls, 1–2μ in diameter, pale blue-green; apices at first straight, later becoming bent, gradually tapering. Sheaths thin, slimy, mostly evident, at length largely confluent. Cells up to 3 diameters in length, 2.5–5.0μ long, not granulated at the cross walls. End-cells pointed, long-conical, neither capitate nor calyptrate. Cell contents mostly homogeneous or finely granular.

Growing in standing fresh and brackish water, on damp earth and wet rocks, in caves and sometimes in total darkness, and in warm springs, this plant is cosmopolitan and tolerant of extremely variable conditions. It has been noted in North America from Alaska to the Barbados, and is well known. Tilden (1898) reported it from the Yellowstone, Lower Geyser Basin, at 33° C., mixed with *P. laminosum* (Ag.) Gom.

While frequent in the Park, it is not conspicuous. It has been noted in the Lower Geyser Basin: White Dome Geyser (no. 404), at 20° C., pH. 8.4; Upper Geyser Basin: Emerald Pool, at 31° C., pH. 8.35; Mammoth Hot Springs: small pool near Soda Spring (no. 126), at 42° C., pH. 6.1;
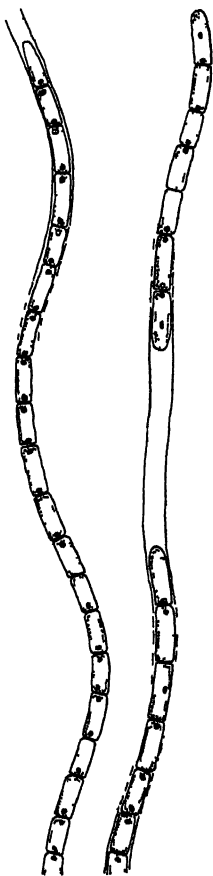
FIG 62 — *Phormidium tenue* var *granuliferum* (× 2000)

Bijah Group: small pool (nos. 118, 119), at 25–47.2° C., pH. 6.1; and in a few other springs. Its observed range of tolerance extended from 20° to 50.7° C., pH. 6.1 to 8.4. Its greatest abundance was noted at 47.2° C., pH. 6.1. In general it was mixed with other species of *Phormidium* and with those of *Oscillatoria*.

8A. Phormidium tenue (Menegh.) Gom.

var. **granuliferum**, var. nov.

Stratum bright blue-green, extended, membranous, and often with erect tufts above. Trichomes flexuous to contorted, lightly constricted at the cross walls, slightly tapering at the apices, 0.9–1.5μ in diameter. Sheaths thin, incompletely confluent but often almost invisible. Cells 2.0–5.5, mostly 2.5–4.0, diameters in length, 2.5–8.5μ in length, mostly with a granule on each side of the cross walls. End-cell long-conical with a rounded apex, without calyptra.

The var. *granuliferum* differs from *P. tenue* in being more slender, in having longer cells, granulated cross walls, and having a less acuminate apex. It is quite close to the species but distinct.

It appears to be limited to the Geyser Basins and a few scattered springs elsewhere. The type (no. 445) was found in a small pool between Oblong and Giant Geysers, in the Upper Basin, growing at 34.9° C. and pH. 8.55. At that place it grew both submerged and on wet rock (no. 444), along with *Scytonematopsis hydnoides* (of this paper), *Mastigocladus laminosus* var. *phormidioides* Boye P., and *Spirulina tenerrima* Kütz. The other localities in which it has been found include:—Upper Geyser Basin: Emerald Pool (no. 353), Handkerchief Pool (no. 351); Ochre Spring (no. 62); Bijah Group: small pot (no. 307); and Twin Buttes Region: Spray Geyser (no. 426). Its observed range of latitude in temperature and acidity is 33–73.6° C., pH. 6.0–8.9. It is more important locally than the species *P. tenue*.

9. Phormidium foveolarum (Mont.) Gom.

Monogr. Oscill., p. 164, 1893.

Stratum thin, gelatinous, dark green to blackish, extended or limited. Trichomes contorted, regularly and deeply constricted at the cross walls, loosely placed, cir. 1.5μ in diameter, pale blue-green; trichomes not tapering at the apices. Sheaths broad, usually completely confluent, colorless. Cells somewhat subspherical, 0.8–2.0μ in length, not granulated at the cross walls; cell contents homogeneous. End-cells unmodified, rounded.

Widely distributed and well known in many regions, it has been reported from North America very few times. Gardner (1903) found it growing with *P. autumnale* (Ag.) Gom. in roadside ditches near LaConner, Washington; and Drouet (1932) recorded its collection by Geisendorfer in Missouri. It has not been noted in thermal sites.

It has been found in a single locality in the Yellowstone, on a wet sinter ledge on the shore of Yellowstone Lake at West Thumb (no. 449), growing with *Calothrix parietina* Thuret and *Nostoc microscopicum* Carm. It was growing at a temperature averaging around 20° C. (in

July). The growth was largely superficial but it also penetrated into the porous, fibrillar sinter 3–4 mm. There was no evidence of its dissolving its way in; rather it grew into already existing cavities. The plant in the Yellowstone, as elsewhere, is essentially non-thermal. Its presence on the ledges kept warm by seepage from nearby hot springs show tolerance for a temperature very slightly above that for meteoric waters. The reaction of the water squeezed from the algae was pH. 7.8.

10. PHORMIDIUM LURIDUM (Kütz.) Gomont

Monogr. Oscill., p. 165, 1892.

Stratum membranaceous, purple to dull violet above, grayish blue-green within. Trichomes somewhat contorted, more or less entangled, lightly constricted at the cross walls, not tapering at the apices, 1.7–2.0μ in diameter, pale bluish-violet. Sheaths thin, soft, difficultly visible, confluent. Cells 1.0–2.5 diameters in length (mostly cir. 1.5 diameters), 1.8–4.7μ long, not granulated at the cross walls; cell contents homogeneous; end-cells unmodified, rounded, neither capitate nor calyptrate.

Fremy's forma *violascens* seems to me to be the species itself, his forma *nigrescens* probably a distinct form that is absent in the Yellowstone, or at least unknown.

Growing in standing water and in warm springs, the plant is widely distributed, but is poorly known in North America. It has been reported from St. Vincent and Dominica, West Indies (W. and G. S. West, 1900; G. S. West, 1904), but not from the continent.

In the Yellowstone it has been found twice in seeps along the Firehole River, Upper Geyser Basin, at 28° and 32.6° C., pH. 8.1 and 8.25.

11. PHORMIDIUM VALDERIANUM (Delph.) Gom.

Monogr. Oscill., p. 167, 1892.

Syn.: *Phormidium Valderiae* (Delph.) Schmidle.

Stratum extended, up to 3 cm. in thickness, lamellate, the upper layers dull green, the lower whitish, slimy-cartilaginous. Filaments densely packed and crowded, flexuous to contorted. Sheaths at first thin and distinct, later confluent and indistinguishable. Trichomes blue-green, 2.0–2.5μ in diameter, lightly constricted at the cross walls, mostly uniformly cylindrical. Cells 3.3–6.7μ in length, mostly with 1–2 granules at the cross walls; cell contents blue-green. Apices unspecialized, not tapering; end-cells rounded, not calyptrate.

Gomont's diagnosis states that the trichomes are not constricted at the cross walls. That is in opposition to his figure of the plant; and in disagreement with the material the author has been able to examine. The change in description has been made to correct this error.

This widely distributed plant is known from a variety of habitats: flowing and standing fresh water, brackish water, wet rocks and timbers, and hot springs. It is rather well known in North America. Butler and Polley (Setchell and Gardner, 1903) found it in a warm sulphur spring in Banff, Alberta, and it was reported (according to Tilden, 1910) from a thermal spring at the foot of the Volcano of the Virgin, Lower California (Mex.) at 75° (C. or F.?). It has not been reported previously from the Yellowstone.

In the Park it is occasional to rare. It was found in the Twin Buttes Region, Spray Geyser (no. 415), at 47.2° C., pH. 8.9, in good quantity; and in the Bijah Group, small unnamed spring (no. 122), at 46° C., pH. 6.1., in small quantity.
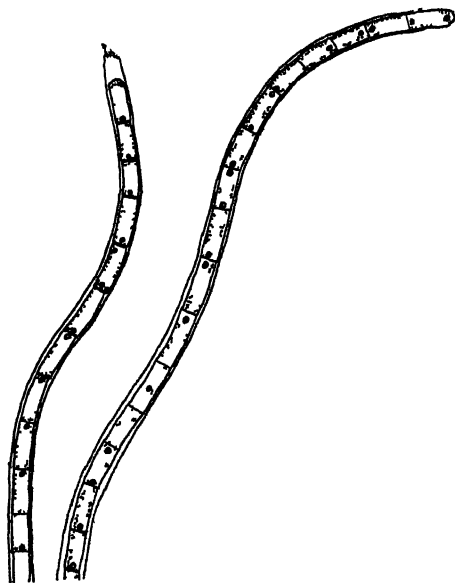
Fɪɢ. 63 —*Phormidium valderianum* var. *cartilagineum* (×1300).

11A. PHORMIDIUM VALDERIANUM (Delph.) Gom.

var. **cartilagineum**, var. nov.

Stratum extended, up to 4 (rarely 5) cm. in thickness; cartilaginous, homogeneous, not lamellate, deep blue-green above, pale blue-green to whitish in lower portions, surface covered with anastomosing wrinkles raised as much as 2 mm. above the general surface. Trichomes 1.3–2.0μ in diameter; cells 3.5–6.0μ in length. Sheaths distinct in part, completely confluent in other parts. Otherwise as in the species.

The variety differs from the species in several respects. Microscopically it is of smaller size but quite comparable. On gross examination its tougher composition, thicker mass, less slimy content, and beautifully marked, richly colored surface make the variety unmistakable. The strata are translucent and give the appearance of deeply pigmented gelatin.

The occurrence of the plant is decidedly limited and, while it is not rare in a few localities, it is local. The most typical site for it is the basal slope of a geyser (or eruptive spring) cone, where the supply of water is rather constant. The alga has been found only where it is frequently sprayed with warm water. Geysers of irregular or infrequent eruption do not favor it. It appears to be confined to basic waters (pH. 7.7–9.1) and sites with a temperature between 40° and 60° C. It can endure severe fluctuations in temperature. The type (no. 435) is from Bijou Geyser, growing (at time of collection) at 44.5° C. and pH. 8.95. Bijou is one of a complex spring group. The chief member, Giant Geyser, is noted as the highest geyser in the world. It has a large broken tower-like cone situated on a broad low mound. In addition to the Giant, there are three smaller geysers: Bijou, Mastiff, and Catfish, as well as at least three small non-eruptive springs. Of these springs, either Bijou or Mastiff is almost always erupting, frequently two of the three are in action, occasionally all three at once. The non-eruptive springs constantly supply a little water. Consequently a supply of water is consistent but the volume and temperature fluctuate almost at random. During the long periods of quiescence of Giant Geyser the temperature of the water reaching the strata of *P. valderianum cartilagineum* never falls below approx. 40° C. and never rises above 60° C. During an eruption of Giant (at intervals of six to fourteen or more days) the living algae are deluged with water above 76° C. without apparent injury—certainly without killing the abundant growth. (It is of interest that *Calothrix Kuntzei* Richter in the same site is killed by this temperature). The alga has been noted in three other sites in the Upper Geyser Basin, and in a single spring in the Twin Buttes Region (Spray Geyser, no. 427, cir. 40° C., pH. 9.0, at the lowest temperature noted during the eruptive cycle.)

12A. PHORMIDIUM TRUNCATUM Lemm.

var. thermale, var. nov.

Stratum often poorly developed, up to 1.5 mm. in thickness, epiphytic on other algae, soft, homogeneous, orange-brown. Trichomes mostly closely packed, wavy to irregularly contorted, rarely parallel, 0 8–1.3μ in diameter,

with indistinct cross walls, not constricted at the cross walls, pale blue-green. Sheaths confluent into an amorphous slimy matrix. Cells cylindrical, 2–4μ in length, mostly with homogeneous contents, sometimes with 1–2 granules; cross walls not granulated. End-cells feebly broadened, truncate to sub-truncate, with slightly thickened end membranes.
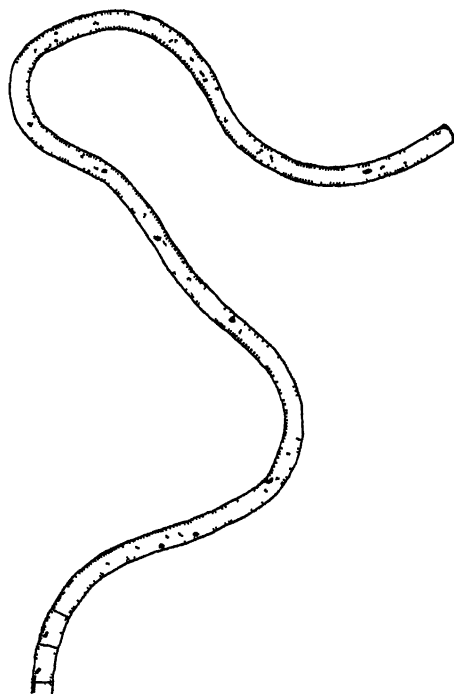
Fig. 64 —*Phormidium truncatum* var *thermale*
(×2800).

The var. *thermale* differs from *P. truncatum* in the color of the stratum, size of the trichomes, entanglement of the filaments, and in the granulation of the cell contents. It resembles it in having distinctive truncate apices and in its general microscopic aspect.

The only locality for it is a small spring on Bijou Geyser cone, Upper Geyser Basin (type: no. 440). It was growing on *Phormidium vesiculosum* (of this paper) and modifying the aspect of that plant very sharply. The normally soft, pale bluish, stalked vesicles were thicker, slightly wrinkled, and were coated with an orange-brown slimy layer. The plants were in shallow water at 48.3° C. and pH. 9.0.

13. PHORMIDIUM RUBRUM Tilden

Bot. Gaz. 25, p. 100, 1898.

Stratum gelatinous, thin to thick, mostly buried or underlying other algae, scarlet, pink, or flesh colored, faintly blue-green tinged when in strong light. Filaments more or less flexuous but not contorted, loosely entangled. Sheaths thin, difficultly visible, mostly confluent. Trichomes 0.9–1.2μ in diameter, fragile, not constricted at the cross walls; apices straight, not tapering. Cells 0 6–1.2 diameters in length; cross walls inconspicuous, not granulated; cell contents dull pinkish-yellow to bluish-green. End-cells rounded, neither capitate nor calyptrate.

This plant was inadequately described from the Yellowstone by Tilden. She found it in the overflow of a small spring between the Upper Basin and the Midway Geyser Basin, growing in tepid water. It has not been reported since then. Her description has been amplified to include a few additional features.

In this study it was noted in the Upper Geyser Basin: Bijou Geyser (nos. 434, 437), at 42–16° C., pH. 8.95, small spring near Grand Geyser (no. 391), at 58° C., pH. 8.05; in the Twin Buttes Region: Spray Geyser (nos. 428, 437), at 33.1–42° C., pH. 8.85–8.95. The alga is one of the most striking plants of the Park, and the color is highly unusual. Unfortunately the preferred habitat, beneath the surface of porous sinter and under the strata of other algae, makes it difficult to find.

14. PHORMIDIUM PURPURASCENS (Kütz.) Gom.

Jour. de Bot. 4, p. 355, 1890.

Stratum leathery, purple to violet-brown. Filaments strongly contorted and interwoven. Sheaths easily visible, thin, later incompletely confluent. Trichomes not constricted at the cross walls, 1.5–2.5μ in diameter, dull violet to bluish violet; apices straight, not tapering. Cells 1–2 diameters in length, 2.0–4.5μ long; cross walls mostly with 1–2 granules on each side; end-cells rounded, neither capitate nor calyptrate.

This probably cosmopolitan species is known from standing water, moist rock cliffs, and hot springs in Europe and North Africa. Tilden (1897) reported it from the Yellowstone. Later (1910) she stated: "Further study proved that the Yellowstone specimens should be placed under *Hypheothrix calcicola* (Ag.) Rab." She thought that her record for *P. purpurascens* should be considered valid, since there might have been a mixture of the two plants!

In the Park it seems to be uncommon. It was noted only in the White Elephant Grottoes at Mammoth Hot Springs (no. 94), at 51.1° C., pH.

7.0.   The author has found the species also at Hot Springs, South Dakota (no. 7), where it grew in great profusion on the cement dam and spillway of a tepid spring at cir. 27.5° C.

14A. PHORMIDIUM PURPURASCENS (Kütz.) Gom.

var. laminatum, var. nov.

Stratum extended, made up of thin gelatinous lamellae interspaced with limy layers, fragile and up to 1 cm. in thickness, purplish-brown.   Trichomes flexuous, often straight, 1.0–1.4μ in diameter.   Sheaths mostly confluent, usually invisible.   Cells 2–4 diameters in length, 2–6μ long.

The more slender trichomes, longer cells, less prominent sheaths, and laminate strata distinguish this variety from the species.

Found generally in the Mammoth Hot Springs, the plant is common and abundant.   It has been observed rarely outside of this limited area. The type (no. 79) is from the Orange Spring Mound, Jr., growing at 55° C. and pH. 6.9.   The springs in which it has been noted include Orange Spring Mound, Jr. (nos. 77, 78, 79, 80, 81, 82), White Elephant Spring, White Elephant Grottoes, Diana Terrace (no. 201), Main Terrace (no. 229), Angel Terrace, Cleopatra Terrace, Hymen Terrace, and others in the Mammoth Group; a single spring in the Meadow Springs Group (no. 185); and a single spring in the Artist's Paintpots (no. 299).   The variety is clearly thermal and is most abundant at temperatures between 45° and 60° C., and at acidities of pH. 6.9–7.6.   It was noted at the extremes of 43.6° C. and 64.9° C., pH. 6.45 and 7.75.

15. PHORMIDIUM RAMOSUM Boye Pet.

Freshw. Cyanoph. Iceland, p. 281, 1923.

Stratum consisting of slender, divided, and branched, taper-pointed, often somewhat confluent or free-waving corded strands up to 15 cm. (or more) in length, usually less, attached variously or arising from an extended basal stratum, blue-green.   Sheaths mostly confluent.   Trichomes parallel or lightly interwoven, more or less straight, not constricted at the cross walls, 1.3–1.9μ in diameter.   Cells 2–3 diameters in length, 2.9–5.1μ long.   Apices straight, not tapering.   End-cells rounded, with thickened end membranes, not capitate.

The plant has been reported only from warm water in Iceland.

In the Yellowstone it has been found in abundance in the quite basic waters of Spray Geyser, Twin Buttes Region (nos. 414, 416, 417, 418, 421, 422, 423).   It grew in the overflow rill of the geyser, and in places almost choked it.   It was in water that at the upper limit of growth of

P. ramosum was at 65° C., pH. 8.6, at the lower limit at cir. 37.4° C., pH. 8.95. The alga extended down the rill to the point of its junction with Imperial Geyser overflow creek, and was present in this stream in small
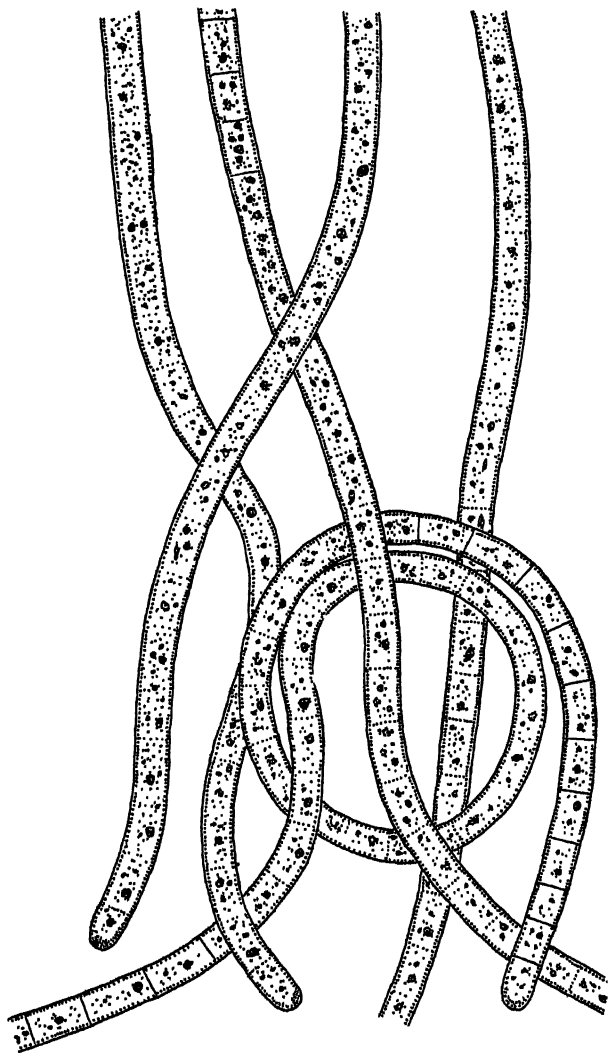
FIG. 65.—*Phormidium acidophilum* (×2140).

quantities for a few hundred yards below. The corded strands of the plant were often covered with epiphytic species of *Synechococcus*. The temperature of the water in Spray Geyser rill is more constant than in

most geyser overflows, due to the almost uninterrupted eruptions. The temperatures given above are the lowest reached during the geyser cycle. The temperature rose 0.9–4.3° C. during the cycle, at various points in the stream. The greatest variation took place at and near the vent.

16. Phormidium acidophilum, sp. nov.

Stratum extended, soft spongy-gelatinous, not lamellate, dull yellowish blue-green throughout, up to 5 mm. in thickness. Trichomes mostly rather thickly placed, entangled and contorted, or less often more or less flexuous and parallel, frequently rolled, not constricted at the cross walls, 1.8–2.4μ in diameter; apices straight, uniform. Sheaths completely confluent, mostly invisible. Cells 1.5–2.5 diameters in length, 2–6μ long; cell contents mostly with coarse granules and always with numerous fine granules, not granulated at the cross walls. End-cells rounded, without calyptra.

There is a close resemblance between *P. acidophilum* and *P. valderianum* (Delph.) Gom. The two may be separated by several criteria. The granular cell contents and ungranulated walls of *P. acidophilum* are in direct contrast to the latter, the less prominent cross walls and sheaths of *P. acidophilum* are distinctive, and the contorted and rolled trichomes are not found in *P. valderianum;* the strata of the species are different in color, texture, and appearance.

The plant has been found in the acid springs of the Mud Volcano Group. The type (no. 68) is from a small unnamed spring just east of the Mud Volcano, where it grew at 40.3° C., pH. 5.1. The species is quite abundant in this group of springs, but has not been found elsewhere. It occurred at from 30.9° C. to 54.7° C., from pH. 4.85 to 5.45, mostly immersed but sometimes on wet mud.

17. Phormidium geysericola, sp. nov.

Stratum tough, fibrous, not lamellate, usually with numerous included granules of silica, up to 3 cm. in thickness, with corded streamer-like projections up to 10 cm. in length and up to 1 cm. in diameter, pale salmon to yellowish, whitish below. Filaments very long, straight, and mostly parallel, not crowded, trichomes not constricted at the cross walls, 0.4–0.6μ in diameter, pale blue-green, often yellowish and almost colorless; apices neither tapering nor capitate. Sheaths hyaline, completely confluent into a generally colorless matrix. Cells 1–2 diameters in length, 0.4–1.0μ long, and not granulated at the cross walls; cell contents homogeneous; cross walls inconspicuous and for the most part difficultly visible. End-cells rounded, unmodified.

P. geysericola is similar to *P. bijahensis* (of this paper) and to *P. subterraneum* (of this paper). The three are readily separated by the ap-

pearance of the strata. In this regard *P. geysericola* is decidedly distinct. Microscopically the trichomes are more parallel in this species than in the other two; they are less crowded and the cells are shorter. The distribution of the three is distinct.

The species has been found in four springs. The type (no. 329) is from Riverside Geyser, Upper Geyser Basin, where it grew on the rim of the geyser indicator. It received water at cir. 79° C. for about two hours before each eruption, and was never below 65° C. (at least for
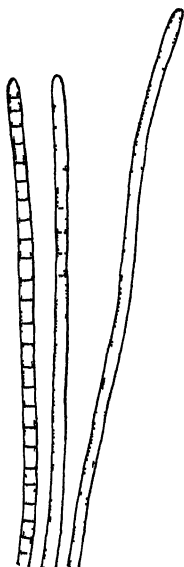
Fig. 66.—*Phormidium gey-sericola* (×3000).

several weeks at a time). The water varied from pH. 8.6 to 8.9 during the approximately seven-hour geyser cycle. A second collection was made in a spring at the edge of the Lower Geyser Basin near the service road that passes along the Fairy Creek Valley. In this spring (nos. 406, 407) the alga was at 78-84° C., and pH. 8.8. The growth in both places was prolific but not extensive. In lesser abundance it has been found in the Twin Buttes Region: Spray Geyser (no. 420), at 69° C., pH. 8.6; and Midway Geyser Basin; Excelsior Geyser Crater (no. 358), at 59.3° C., pH. 8.3. The species seems to occur only in very specialized habitats, where the water is hot and agitated; it is a well marked thermal limital species.

18. Phormidium subterraneum, sp. nov.

Stratum extended, soft leathery, up to 1.5 mm. thick, easily torn, surface sometimes tomentose with dendritic lime; yellowish green to grayish within. Trichomes more or less parallel or irregularly disposed, often contorted, densely packed, cir. 0.4μ in diameter, not constricted at the easily visible cross walls, yellowish green; apices straight, not tapering. Sheaths confluent, invisible, without pigmentation. Cells 2–3 diameters in length; end-cells rounded, not calyptrate.

This species resembles *P. bijahensis* (of this paper), but is easily separated from it by the non-pigmented matrix, the texture of the stratum, and by the easily visible cross walls. The two cannot be confused either microscopically or in nature.

The plant was first encountered in the Sunken Spring, Mammoth Hot Springs (type: no. 143), at 41° C., pH. 6.35. Here it formed an almost pure stratum in a spring pool. The spring occupies a pit-shaped sink about five feet deep, and has no above-ground outlet. The water is mostly a few inches deep, and the algal growth overlaid a soft muddy marl in the shallow water. It has been found also in the Artist's Paint Pots: small spring (no. 298), at 62.1° C.; Elk Park: spring in north-east section (nos. 215, 216, 217), at 63-72.4° C., pH. 8.15–8.25; and in the Meadow Springs: two small springs (nos. 190, 193), at 63.5° C. and 62.2° C., pH. 6.95 and 5.4. The plant grew in the spring pools in every case, and was sharply limited to quiescent waters.

19. Phormidium bijahensis, sp. nov.

Stratum salmon-pink, flesh-colored or red, often mixed with other algae or poorly developed, up to 2 mm. in thickness, soft spongy to flocculent; at high temperatures filaments often free or in small clumps. Filaments packed, twisted and contorted, or for short distances straight to flexuous, with completely confluent sheaths. Sheaths thin, soft, confluent into a general homogeneous matrix, hyaline or in masses pinkish. Trichomes twisted, often crooked, rarely straight, 0.3–0.5μ in diameter, long or at high temperatures often fragile and short, not constricted at the cross walls. Cells 1.5–3.0 diameters in length, pale blue-green, with inconspicuous cross walls. Apices straight, not tapering; end-cells rounded, unmodified.

This very minute species is distinct. In dimensions it comes close to *P. geysericola* (of this paper) and *P. subterraneum* (of this paper). Its stratum is quite different from these, and its distribution is different.

Up to the present the plant has been noted in the Bijah Spring Group: Bijah Spring (nos. 122, 129, 130, 131, 132, 133); Lower Geyser Basin: Five Sisters' Springs (no. 397); Midway Geyser Basin: Excelsior Geyser Crater (no. 358); and the Meadow Springs: unnamed spring (no. 180).

In the Bijah Spring it was very abundant and extended from the spring crater at a temperature of 78.5° C. down the overflow rill for several yards to water as cool as 39.8° C. In the Five Sisters' Springs it grew in water at 82° C. and in one of the Meadow Springs in water at 85.2° C. This extraordinarily high thermal tolerance places it in the group of species that includes *Oscillatoria filiformis* (of this paper), up to 85.2° C., *Phormidium geysericola* (of this paper), up to 84° C., *Synechococcus eximius* (of this paper), up to 81° C., and *Pluto caldarius* (Tilden), up to 80° C. At temperatures of 75° C. and above the strata of the plant are poorly developed and involution forms are frequent. Its best growth occurs at cir. 60° C. It has been noted in waters with acidities ranging from pH. 8.3 to 6.1. (Bijah Spring has water that varies from pH. 7.1 at the vent (79° C.) down to pH. 8.65 at the terminus of its main overflow rill (21.2° C.). The type (no. 132) grew at 64.1° C. and pH. 7.95, in the Bijah overflow. The plant is clearly a thermal limital species.

LYNGBYA Agardh

Syst. Alg., p. 25, 1824.

Trichomes single in thin to moderately thick, firm, distinct sheaths, which are either homogeneous or lamellate, colorless or less often pigmented. Filaments straight, flexuous, contorted, or spirally twisted, attached basally, laterally for their entire length, or in the middle, or mostly without any method of attachment, united into more or less definite strata, scattered or solitary. Trichomes sometimes constricted at the cross walls; apices often specialized and end-cells sometimes calyptrate.

The division of the group into the subgenera *Heteroleibleinia, Leibleinia, Spirocoleus,* and *Eulyngbya* (Geitler, 1932) is of assistance in the handling of the group. All of these sections are represented in the Yellowstone.

Unlike the allied genera *Phormidium* and *Oscillatoria, Lyngbya* is unimportant in the thermal springs. Of the close to one hundred species, only seven have been noted in thermal water. These species: *L. maior* Menegh., *L. nigra* Ag., *L. Martensiana* Menegh., *L. lutea* (Ag.) Gom., *L. Molishi* Vouk, *L. thermalis* Rab., and L. *aestuarii* Liebm., are with exceptions known from very few warm springs, and from moderately warm water only. There are no records of thermal forms from the United States. The plants are found in salt, brackish, and fresh water, free-floating or attached, often epiphytic, or on damp soil, rocks, etc. A few are planktonic.

In the springs of the Park *Lyngbya* is poorly represented by unimportant, mostly transitional thermal types.

<div style="text-align:center">KEY TO THE YELLOWSTONE SPECIES.</div>

I. Filaments attached by the base, erect.   *L. Kuetzingii* 1.

II. Filaments not basally attached, but often attached by the middle or broadly, or without attachment.

    1. Filaments definitely attached to the substratum.

        A. Cells 1–2μ long.   *L. epiphytica* 2.

        B. Cells 2.5–6.0μ long.   *L. calotrichicola* 3.

    2. Filaments not regularly attached, often in attached strata.

        A. Filaments spirally twisted.   *L. subspiroides* 4.

        B. Filaments not spirally twisted, often contorted.

            a. Filaments planktonic; with pseudovacuoles. *L cryptovaginata* 5.

            b. Filaments not planktonic; without pseudovacuoles.

                *. Trichomes 3.5–4.0μ in diameter; filaments 3.6–5 0μ in diameter.   *L. Kuetzingiana* 6

                **. Trichomes 4–6μ in diameter; filaments 5–7μ in diameter.

                                L. aeruginео-caerulea 7.

<div style="text-align:center">1. LYNGBYA KUETZINGII Schmidle</div>

<div style="text-align:center">Allg. Bot. Zeitschr., p. 58, 1897.</div>

Syn.: Leibleinia Martensiana Kützing, Bot. Ztg. 5, 1847.

Filaments attached by a basal end, erect, straight or nearly so, stiff, solitary or gregarious, 2–3.5μ in diameter, mostly short and 30–70μ long. Sheaths narrow, firm, colorless, often extending beyond the trichome end. Trichomes 1.5–2.0μ in diameter, not constricted at the cross walls; pale blue-green. Cells 0.3–0.6 diameter in length, not granulated at the cross-walls; end-cells rounded, unspecialized. Hormogonia produced at apices of filaments.

Growing mostly on filamentous algae in standing and slowly flowing water, this plant has not, to my knowledge, been reported from North America. This absence of record is probably due to its small size rather than its rarity. The author has noted it at Falmouth, Massachusetts, in several ponds, growing on *Scytonema crispum* (Ag.) Born. and on rocks.

In the Park it is common in all the larger ponds and lakes, except those of abnormal acidity or excess silt. In semi-thermal waters it is locally abundant. It has been noted in sites with elevated temperatures in the Upper Geyser Basin: Firehole River opposite Biscuit Basin (nos. 431, 432) on *Cladophora,* at 22.5° C., pH. 8.2; and at Mammoth Hot Springs: Jupiter Terrace (no. 238) on *Calothrix thermalis* (Schw.) Hansg., at 20° C., pH. 8.3. It is evidently strictly non-thermal and barely finds a foothold in the cooler waters of some springs.

<div style="text-align:center">2. LYNGBYA EPIPHYTICA Hieron.</div>

<div style="text-align:center">in Engler-Prantl, Nat. Pflanzenf. I, 1, a, p. 67, 1898.</div>

Filaments epiphytic, attached for their entire length, twisted around other filamentous algae in close or loose spirals, 1.5–2.0μ in diameter. Sheaths

thin, colorless. Trichomes 1.0–1.5μ in diameter, not constricted at the cross walls; apices unspecialized. Cells 1–2μ in length, not granulated at the cross walls; end-cells rounded.

Cosmopolitan on filamentous algae (*Lyngbya, Oedogonium, Cladophora, Scytonema*, etc.) in standing and flowing fresh water, less often in brackish and salt water, it is difficult to understand the scarcity of records for North America. Setchell and Gardner (1919) reported it from the Pacific coast. It has not been noted inland. The author has found it in Massachusetts, New York, Indiana, and Wyoming in cool water.
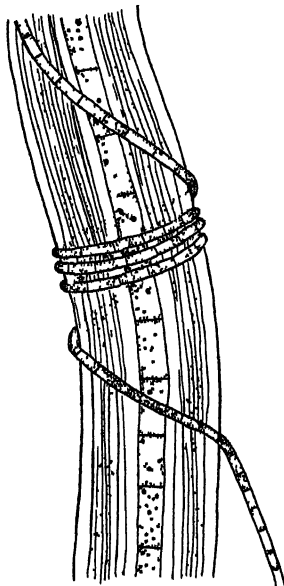
Fig. 67 —*Lyngbya calotrichicola*, on filament of *Calothrix Baileyi* (×830).

In the Yellowstone it is commonly present in the rivers but is absent from truly thermal sites. It was found in the Firehole River opposite the Biscuit Basin (no. 132) at 22.5° C., pH. 8.2. At this point the water is feebly warmed by overflows from the geysers and hot springs, and several typical thermal algae were present.

3. Lyngbya calotrichicola, sp. nov.

Filaments on and among other filamentous algae, in part wound in close spiral coils around the filaments, in part loosely and irregularly twisted around them, and in part irregularly disposed on and between them. Sheaths thin, colorless, difficultly visible. Trichomes 1.3–1.6μ in diameter, not con-

stricted at the cross walls, pale blue-green; apices unspecialized. Cells 2–4
diameters in length, 2.5–6.0µ long, not granulated at the often inconspicuous
cross walls; end-cells rounded.
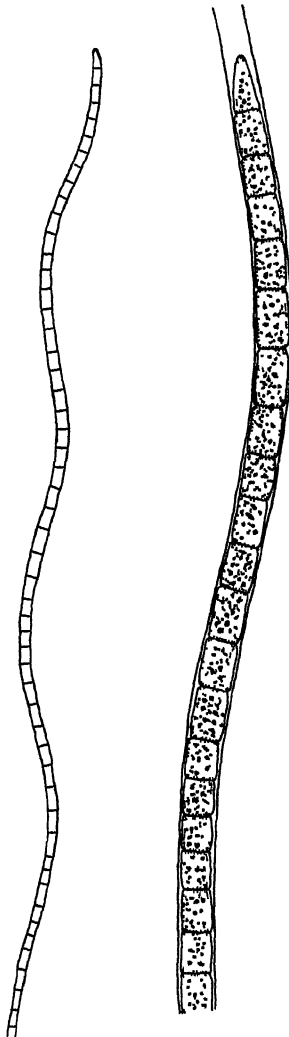
FIG. 68.—*Lyngbya subspiroides,*
left, filament showing lax spiral
twisting (×325); right, tip of
trichome (×1250).

This alga, while close to *L. epiphytica Hieron.* and its var. *aquae-dulcis*
Gardner, is readily separated from them by its long cells.

It has been found upon and among *Calothrix Baileyi* (of this paper) in great profusion at the Boiling River near the small falls at its mouth (type: no. 261), at 35.2° C., pII. 6.6. The *Calothrix* was on the wet bank of the stream and on rocks in the stream bed, where it received the warm spray from the falls. The *Lyngbya* was in part in such abundance that many of the filaments were among and between the *Calothrix* rather than on it. Where it occurred in lesser profusion, it was regularly epiphytic. The growth of the *Calothrix* (all of which was infested) extended for quite an area, and the temperature varied from cir. 26° C. to cir. 40° C.

4. Lyngbya subspiroides, sp. nov.

Filaments epiphytic on the strata of gelatinous Myxophyceae, long, up to 2 mm. in length, loosely spirally twisted or sometimes irregularly contorted, 3.5–4.8μ in diameter. Sheaths very thin, often almost invisible, firm, homogeneous, hyaline. Trichomes very feebly constricted at the cross walls, 3.3–4.2μ in diameter. Cells cylindrical, 1¼–2 diameters in length. 3.6–10μ long; cell contents bright blue-green, granular, not granulated at the cross walls; end-cell elongate, conical with a narrowly rounded unthickened apex, up to 9μ in length. Hormogonia long.

This species is quite distinct from the other members of the genus.

L. subspiroides is known from a single collection only. The type material (no. 320) was found growing in a mixed stratum of *Cylindrospermum stagnale* (Kutz.) B. & F. and *Mastigocladus laminosus* Cohn in shallow water in a small seep on the side of Imperial Geyser crater, Twin Buttes Region, at 41° C.

5. LYNGBYA CRYPTOVAGINATA Schkorb.

after Geitler in Pascher, Süsswasserfl. 12, p. 401, 1925.

Filaments solitary, free floating, straight, 4–9μ in diameter. Sheaths colorless, homogeneous, delicate, at first difficultly visible, at length evident. Trichomes 4–7μ in diameter, lightly constricted at the cross walls, blue-green; apices unspecialized. Cells 0.5–1.0 diameters in length, with pseudovacuoles. End-cells rounded.

This poorly known species was described from H_2S–containing water in Ukraine, and has not been reported since.

Found in abundance in the Firehole River opposite the Biscuit Basin (no. 132) at 22.5° C., pII. 8.2, this plant has little claim for recognition as a thermal alga.

6. LYNGBYA KUETZINGIANA Kirchn.

Alg. Schles., p. 242.

Stratum membranous, lamellate, bright to olive blue-green above, paler and almost colorless within. Filaments 3.6–5.0μ in diameter, contorted. Trichomes

blue-green, 3.5–4.0µ in diameter, lightly constricted at the cross walls in the apical portions, elsewhere not constricted. Cells cir. 1 diameter in length, granulated at the cross walls. Apices not tapering; end-cells blunt conical or rounded, not calyptrate.

Growing on moist soil, on wet rocks and among mosses, this plant has been known only from Europe.

In the Yellowstone it has been found on the wet walls of the Stygian Caves (shaded) at Mammoth (no. 151), at 10.8° C., pH. 7.65; and on the base of the Riverside Cone, Boiling River Group (no. 272), at 16.9-23.8° C. In both sites it formed unmixed strata.

7. Lyngbya aeruginco-cacrulca (Kütz.) Gomont

Monogr. Oscill., p. 146, 1892.

Stratum dull blue-green to blackish, or filaments scattered. Filaments flexuous to contorted, 5–7µ in diameter. Sheaths thin, firm, homogeneous, colorless. Trichomes 4–6µ in diameter, not constricted at the cross walls, pale blue-green. Cells 0.5–1.0 diameter in length, 2.3–6.0µ long, with cross walls sometimes granulated and conspicuous, sometimes inconspicuous and not granulated. Apices not tapering; end-cells obtusely conical or rounded, rarely feebly capitate (?), with feebly thickened membranes.

Growing in standing or flowing fresh water, often on dead waterplants, rarely on wet mud, it is cosmopolitan. It is frequent in the United States, and has been reported by W. and G. S. West (1900) from a warm stream in Dominica, West Indies.

In the Park it has been found in the Upper Geyser Basin: cool spring (no. 335), at 17.9° C., pH. 7.6; and in the Lower Geyser Basin: White Dome Geyser (no. 405), at 19.2° C., pH. 8.4. In the former site it formed a pure growth, in the latter it was mixed with other Myxophyceae. The plant is at most a feeble invader of thermal situations.

POLYCHLAMYDUM W. & G. S. West

Jour. Bot. 35, p. 271, 1897.

Trichomes single or occasionally 2–3 in very thick, lamellate sheaths. Inner layers of sheaths firm and often brownish; outer layers gelatinized and always colorless, often uneven. Filaments straight or flexuous. Hormogonia present.

Type species: *Polychlamydum insigne* W. & G. S. West.

Of the three species of the genus, *P. insigne* was found on water plants in a lake in Africa, *P. varium* Ghose was noted on the bark of trees in

India, and *P. calcicolum* Kuff. was described from a waterfall in Luxemburg and subsequently found at the Mammoth Hot Springs in the Yellowstone.

In the Yellowstone the genus is unimportant.

A single Yellowstone species.

1. POLYCHLAMYDUM CALCICOLUM Kufferath

Ann. biol. lac., 1914.

Filaments cir. 30μ in diameter by mostly cir. 300–320μ in length. Trichomes single in the filaments, cir. 4μ in diameter, blue-green, tapering gradually toward the ends. End-cells subtruncate. Trichomes more or less constricted at the cross walls. Cells 3–8μ in length. Sheaths very thick, cir. 12–13μ, lamellate with the inner layers firm, the outer softer and gelatinous, colorless, with smooth surfaces.

There seem to be just two records for the plant: it has been found in the lime incrustation in a waterfall in Luxemburg, and in the lime depositions of Jupiter Terrace, Mammoth Hot Springs, Yellowstone. The latter record was made by Prát (1929).

In the present study the plant has been found once, in Angel Terrace, Mammoth Hot Springs, growing with species of *Phormidium* and *Calothrix thermalis* (Schw.) Hansg. at 28.6° C. and pH. 8.15. From Prát's observation and from the single collection above, it seems probable that the plant is generally present in the springs at Mammoth, but it is not abundant.

SYMPLOCA Kützing

Phyc. gen., p. 201, 1843.

Trichomes solitary in thin sheaths. Filaments sometimes with false branching, united into extended strata, at first prostrate, later in part united into numerous erect (or less often prostrate) fascicles that arise from the stratum as conical, often anastomosing tufts. Sheaths firm or somewhat slimy, often laterally confluent except at tips. Trichomes straight, often feebly tapering; end-cells never capitate but often lightly calyptrate.

The majority of the species are subaerial, several occur in fresh water, several in salt water, and six have been reported from warm and hot springs. The known thermal species are: *S. thermalis* (Kütz.) Gom., *S. dubia* (Naeg.) Gom., *S. Menegheniana* Kütz., *S. Yappii* G. S. West, *S. elegans* Kütz., and *S. Nemecii* Prát. Of these only *S. Nemecii* has been recorded from thermal waters in the United States.

In the Park four very conspicuous but quite infrequent species occur.

I. Trichomes 2.8μ in diameter or greater.
  1. Trichomes 4.5–5.5μ in diameter; not constricted at the cross walls.
                              S. muscorum var. *caldariorum* 1A.
  2. Trichomes 2.8–3.4μ in diameter; feebly constricted at the cross walls.
                              S. cavernarum 2.
II. Trichomes 2μ in diameter or less.
  1. Trichomes 1.3–2.0μ in diameter; cells 3–7 diameters in length.
                              S. elegans var. *pulcherrima* 3A.
  2. Trichomes cir. 1μ in diameter; cells 0.7–1.5 diameters in length.
                              S. Nemecii 4.

1A. SYMPLOCA MUSCORUM (Ag.) Gom. var. CALDARIORUM Lemm.

Krypt.-Fl. Mark Brandenb. 3, p. 143, 1910.

Stratum pale blue-gray to bluish violet, leathery. Filaments contorted, twisted, united into mostly prostrate fascicles that are more or less confluent into a plane stratum. Sheaths thin, firm to soft and confluent, up to 2μ thick. Trichomes 4.5–5.5μ in diameter, not constricted at the cross walls. Cells 1–2 diameters in length, 4.5–10μ long, pale steel-blue; end-cells broadly rounded, often feebly calyptrate.

Known from greenhouses in Europe, this plant is new to the North American flora.

It has been noted a single time in the White Elephant Grottoes at the Mammoth Hot Springs (no. 91), at 28° C., pH. 8.1. In that place it covered several square feet of moist shaded rock.

2. Symploca cavernarum, sp. nov.

Stratum extended, cartilaginous, up to 1 cm. in thickness, dark blue-green to steel-blue, whitish beneath, with massive bundles of filaments up to 2 cm. in length and as much as 2 cm. in diameter at base, tipped with few to numerous slender, free fascicles 3–5 mm. long and up to 1 mm. in diameter at base. Filaments thickly interwoven, entangled below, and more or less parallel above, 3.8–5.0μ in diameter, with occasional branching. Sheaths firm, distinct, homogeneous, colorless, often empty in basal parts and at tips of fascicles. Trichomes steel-blue, feebly constricted at the thick cross walls, 2.8–3.4μ in diameter. Cells with homogeneous or sparsely granular contents, 1.5–3.5 diameters in length (mostly cir. 2 diameters); end-cells broadly rounded, neither capitate nor tapering, with unthickened membranes. Hormogonia 2–many celled.

This species is quite distinct. Its recognition without microscopic examination is easy, due to the peculiar massive and often botryoidal masses upon which the majority of the fascicles are borne. When the plant is found upon the roofs of caves, the fascicles are pendant from stalactitic, tapering basal masses; when on vertical walls, they are at right angles to

the surface and arise from rounded masses; and when on the upper surfaces of rocks, etc., the erect fascicles arise from low, rounded masses. The orientation seems to be definitely at a right angle to the substratum.
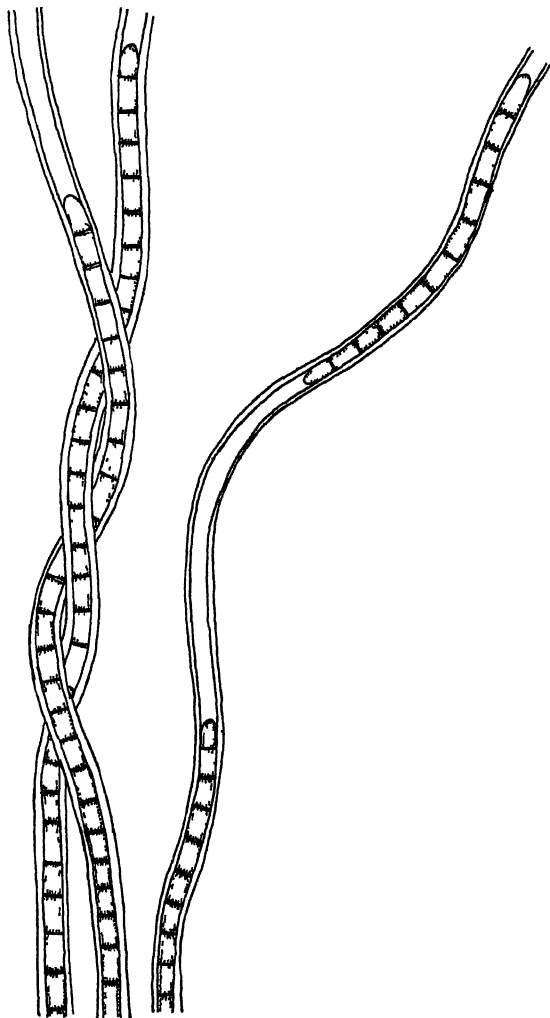
FIG. 69.—*Symploca cavernarum* (×1000).

The species inhabits, so far as is known, caves and other deeply shaded situations. It has been found only in the region around the Mammoth Hot Springs and Boiling River. It grew in the Stygian Caves and the White Elephant Grottoes at Mammoth, and in the Boiling River Caves.

The type (no. 95), from the White Elephant Grottoes, was at 19° C. and pH. 8.1. The plant has been observed at temperatures from 16° C. to 28.5° C., and in alkaline conditions, pH. 7.6–8.1.

3A. SYMPLOCA ELEGANS Kützing

var. **pulcherrima**, var. nov.

Stratum extended, lightly incrusted with silica in the lower portions, orange-brown on surface to whitish within, bluish-green in lower portions, bearing erect fascicles that are more or less completely anastomosed into taper-shaped and often adherent processes up to 2.5 cm. in height, fibrous-gelatinous, often brittle. Fascicles with filaments parallel, erect; basal stratum with filaments contorted and interwoven. Sheaths moderately thick, firm. Trichomes 1.3–2.0µ in diameter. Cells elongate, 3–7 diameters in length, not constricted at the cross walls, mostly with a single granule of considerable size on each side of the cross wall. End-cells slightly narrowed, apices rounded.

The variety differs from *S. elegans* in the length of the cells, and in the color and structure of the stratum. The plant is strikingly handsome. Its richly colored chocolate-brown and orange-brown strata clothe the pools of several hot springs in the Upper Geyser Basin, and aid in their often notable ornamentation. The height of the erect tufts is unusual and the plant is regularly noted by the casual visitors in the Yellowstone. It seems inconceivable that no botanist should have noticed the plant previously. The lack of recognition of the plant cannot be attributed to confusion with other species of *Symploca*—the genus had not been reported from the Park until 1929.

It has been found in basic waters of the Upper Geyser Basin: Wave Pool (type: no. 388), Bijou Geyser (no. 438), Chromatic Spring, Maggie Pool, and Beach Spring. It was in water at 37–43.5° C., pH. 8.1–8.95.

4. SYMPLOCA NEMECII Prát

Studie o Biolithogenesi, Nák. České Ak., p. 98, 1929.

Stratum blue-green to orange-brown, extended or often poorly developed, with erect conical tufts made up of confluent fascicles of filaments; erect tufts up to 5–8 mm. high, flattened or fluted; fascicles anastomosing. Filaments contorted and thickly interwoven below, straight and parallel above, mostly confluent. Trichomes very pale blue-green, scarcely or feebly constricted at the cross walls, 0.8–1.3µ in diameter. Cells 0.7–1.5 diameters in length; end-cells rounded or bluntly pointed, not calyptrate. Sheaths colorless to very faint orange, smooth, soft.

Prát studied this plant in pure culture; his material was secured from the Yellowstone, where he found it in warm and cool waters in the travertine deposits of Jupiter Terrace, Mammoth Hot Springs.

It has been noted in Jupiter Terrace, Main Terrace, and in the Blue Pools at Mammoth, growing in shallow water at 27–39.7° C., pH. 7.3–8.05. The strata rarely occur in an unmixed state but, when they do, the alga is handsome. The stratum is frequently indurated with lime. The plant in nature is somewhat more variable than Prat's observations on it in culture indicate. His description has been modified in a few respects to cover these features.

Cyanohydnum, gen. nov.

Stratum bracket-shaped, laterally attached, fibrous-cartilaginous to gelatinous, with a distinct outer membrane, firm, bearing on the lower surface numerous, slender fascicles of filaments that become detached and serve to propagate the plant. Filaments entangled along face of attachment of thallus, straight and parallel and rather distant in body of thallus, twisted and close in ventral fascicles. Sheaths more or less confluent into a general matrix. Trichomes Phormidium-like. Hormogonia absent.

Type species: *Cyanohydnum cilialum.*

The general aspect of the plant body of *Cyanohydnum* recalls the laterally attached bracket fungi of the Hydnaceae. However, the much thicker, more massive body makes the analogy a little distant. While unmistakably related to such Oscillatoriaceous genera as *Phormidium* and *Symploca,* the structure of the thallus is distinctly more specialized (and along different lines) than in these genera. The plant is one of the most unusual of the Myxophyceae.

A single species.

1. Cyanohydnum ciliatum, sp. nov.

Thallus bracket-shaped, sessile, attached broadly and projecting freely away from the support, cartilaginous to firm-gelatinous, obscurely fibrous with the fibers more or less radiating from the region of attachment, orange-brown to yellowish brown, often whitish at attachment surface, with numerous fine capillary, often branching, flexible blue-green fascicles on the ventral surface. Outer membrane firm and distinct except below and at region of attachment. Brackets up to 4 cm. broad (mostly cir. 3 cm.), up to 15 cm. long (often appearing of indefinite length due to confluence), up to 3 cm. in thickness at region of attachment, and rapidly tapering to cir. 8 mm. in thickness at the edge; ventral surface mostly sloping. Ventral process 2–5 mm. long, very slender, up to 150μ in diameter, with numerous trichomes twisted into irregular rope-like branching strands, clothing the surface with a fur-like blue-green layer; easily detached at maturity. Sheaths incompletely confluent into a general matrix; matrix very pale buff. Trichomes mostly straight and parallel, somewhat distant, in region of attachment entangled and dense, in ventral processes more or less twisted and dense, 1.0-1.3μ in diameter, not at all or very slightly constricted at cross walls.

Cells 2–4 diameters in length; cross walls often marked by a granule on each side; cell contents pale blue-green. Apices unspecialized; end-cells rounded, not calyptrate.
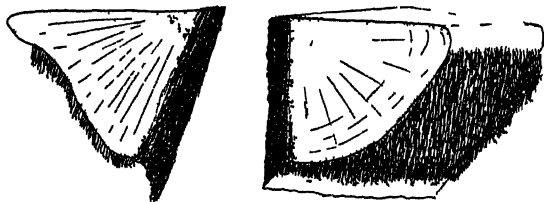
FIG. 70.—*Cyanohydnum ciliatum,* left, section through thallus, right, portion of thallus (diagrammatic) (×1).

Along the edges of the rill of Spray Geyser and of Imperial Geyser overflow creek, Twin Buttes Region, *Cyanohydnum ciliatum* forms an almost continuous projecting ledge wherever the temperature and other factors are favorable. In general it was attached to vertical sinter faces and exposed to strong current. The type (no. 311) was at 51° C., pH. 8.8, and was selected from the best portion of the growth. The total of the plant in this region was approximately 280 running feet of mostly confluent thalli. The bracket-shaped plants were so situated that the upper surface was exactly at water level. (There is little or no variation in the level of the two streams because the flow from the supplying springs is very uniform. Imperial Geyser was very active for the first year of its life, 1928, but more recently it has been a quiescent hot spring. Spray Geyser, in opposition, erupts almost continuously.) The exact shape of the thalli varied with the contour of the bank and the pitch of the rock to which they were attached. The majority of the material examined was heavily infested with *Synechococcus arcuatus* (of this paper) and lightly so with various other Myxophyceae. Immature thalli were easily recognizable by gross or microscopical examination, although the generic features had not yet developed. The plants apparently are long-lived and can produce the ventral processes continuously for at least a few months. The temperature range noted for the plant was cir. 46–59° C. The reaction of the water varied from pH. 8.65 to 8.85. The plant has not been encountered elsewhere and it may be absent from other springs in the region.

SCHIZOTHRIX Kützing

Phyc. gen., p. 230, 1843.

Trichomes single or more often few to many in a sheath. Filaments mostly united into definite or extended strata, less often solitary; strata mostly

attached, rarely free floating, leathery, membranous, felt-like, cushion-like or cacspitose, frequently with erect fascicles arising from the surface. Sheaths moderately soft to firm and tough, never confluent, thin to thick, homogeneous or lamellate, colorless or pigmented. Filaments richly to very sparingly branched.

The division of the group into the subgenera *Symplocastrum* (stratum bearing erect fascicles; sheaths colorless), *Hypheothrix* (stratum leathery; filaments densely interwoven; sheaths mostly colorless), *Inactis* (stratum cushion-like; filaments cacspitose, erect; sheaths mostly colorless), and *Chromosiphon* (filaments single or in variable strata; sheaths pigmented) is of considerable value in the handling of the seventy or more recognized species. Many authors including Tilden (1910) and Gardner (1927) have recognized these divisions as genera. Their treatment is logical and there is little at stake in the matter. When the divisions are elevated to genera, *Schizothrix* is limited to the *Chromosiphon* species.

The species vary greatly in habitat. The majority grow in fresh water, standing or flowing, many on damp soil, rocks, bark, etc., a few are marine, a few epiphytic, at least one endophytic, and six have been recorded from thermal waters. The thermal forms are *S. fragilis* (Kütz.) Gom., *S. tenuis* Woron., *S. panniformis* Rab., *S. calcicola* (Ag.) Gom., *S. penicillata* (Kütz.) Gom. and *S. hawaiensis* Lemm. Of these only *S. calcicola* has been recorded from warm springs in North America.

In the Yellowstone the genus is not important. Four rather local species have been encountered in the investigation, representing the subgenera *Hyphoethrix* and *Chromosiphon*.

<div align="center">KEY TO THE YELLOWSTONE GENERA</div>

I. Sheaths colorless.
  1. Trichomes 1.0-1.7μ in diameter.   *S. calcicola* 1.
  2. Trichomes 3.0μ or greater in diameter.
    A. Sheaths homogeneous.   *S. cyanea* 2.
    B. Sheaths lamellate.   *S. constricta* 3.
II. Sheaths pigmented.   *S. thermophila* 4.

<div align="center">1. SCHIZOTHRIX CALCICOLA (Agardh) Gom.</div>

<div align="center">Monogr. Oscill., p. 307, 1892.</div>

Stratum extended, not indurated (or feebly so), leathery gelatinous, at first thin and blue-green, later often thick and dark to blackish blue-green, sometimes yellowish. Filaments densely and intricately interwoven, twisted and contorted, very sparingly branched. Sheaths colorless, firm. of variable thickness, smooth and thin at first. thicker, feebly lamellate and roughened at maturity, with mostly a single trichome, sometimes with two and occasionally

with several. Trichomes 1.0–1.7μ in diameter, not or sometimes feebly constricted at the often granulated cross walls. Cells 2–6μ long, with blue-green often granular contents, single granules on each side of cross walls often large and conspicuous.

Growing on wet and dripping rocks, in small temporary rock pools, and in greenhouses, *S. calcicola* is known from numerous localities. It is probably cosmopolitan. It has been reported from thermal habitats in North America and Europe. Its presence in the Yellowstone flora has been based on the record of Tilden (1897). She first reported her material as *Phormidium purpurascens* (Kütz.) Gom., later the record was corrected. Her report is of interest. She found it as a component of algal stalactites in a cave in the Lower Geyser Basin. The cave contained the vent of a hot spring, which splashed hot water over the stalactites at short intervals.

In the present investigation it has been noted frequently in non-thermal habitats and a few times in subthermal situations. In the White Elephant Grottoes, Mammoth Hot Springs (no. 93) it was growing on the wet walls at 26° C. Elsewhere the plant grew in cooler sites. The acidity range observed was pH. 6.9 to 8.1.

2. SCHIZOTHRIX CYANEA Naegeli

in Kützing, Spec. Algarum, p. 269, 1849.

Stratum extended, leathery, rusty black to dull blue-green within. Trichomes thickly interwoven, constricted at the cross walls, 3.2–3.7μ in diameter, bright bluish. Filaments cir. 6.5μ in diameter. Sheaths thick, colorless, smooth, homogeneous.

Known only from Central America and Europe, this species is found on moist rocks.

In the Stygian Caves and on damp travertine in their immediate vicinity (Mammoth Hot Springs) it occurs in some profusion. The rocks of the shaded shallow grottoes are damp with cooled thermal water and in the sites occupied by *S. cyanea* (nos. 146, 147) were at 12.8–14° C., pH. 8.1. Elsewhere in the Park the alga is rare or at least has not been found in abundance.

3. Schizothrix constricta, sp. nov.

Stratum extended, orange-brown to bluish buff, up to 1 cm. or more in thickness, lamellate, the upper portion colored, the lower white and with mostly empty sheaths, vertically fibrous, heavily impregnated and incrusted with lime except for the cartilaginous surface layer of cir. 1.0–1.5 mm. Filaments closely packed, straight to flexuous and erect in upper portions, contorted below, 6–14μ in diameter by up to 5mm. long, sparingly to rarely

branched, containing mostly a single trichome, rarely 2–3. Trichomes 3.0–4.2µ in diameter, not especially uniform, cylindrical or less often submoniliform, constricted at the thick cross walls. Cells cylindrical, often swollen, 1.5–5.0 diameters in length; contents homogeneous or with occasional granules, dull blue-green to greenish in color. Sheaths firm, lamellate, hyaline or sometimes yellowish, 1.3–5.0µ thick, lamellae of variable thickness, very distinct; sheaths for the most part cylindrical and smooth, but constricted at frequent intervals, and sometimes with close series of transverse girdles, outer lamellae occasionally flaring.
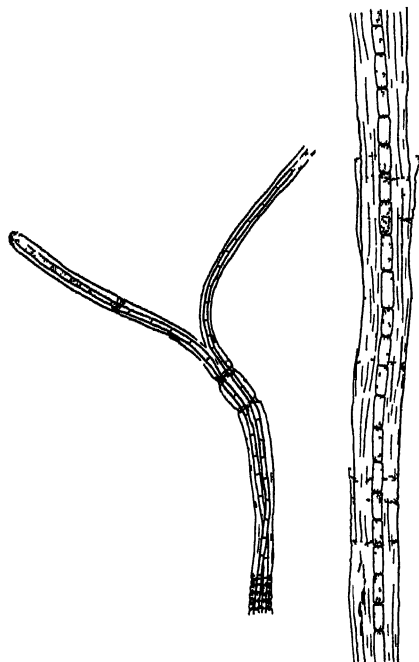
Fig. 71.—*Schizothrix constricta*, left, branched filament with constrictions (×165); right, filament with flaring outer lamellae (×450).

This plant falls in the subgenus *Hypheothrix* and appears to be close to *S. Naegelii* (Kütz.) Geitler, or as close to it as to any in the genus. From this species it is separated by its longer cells, its often colored sheaths, its larger trichomes, its thick end walls, and its habitat.

The only region in which it has been found is the Boiling River section of the Gardiner Canyon. The type (no. 270) is from the Riverside Cone, where it grew at 24° C., pH. 6.6, on wet travertine. The species seems to favor deep shade and moist, not wet, situations at moderate temperatures, 22–31° C.

4. Schizothrix thermophila, sp. nov.

Stratum extended, felt-like and leathery, up to 4 mm. in thickness, dark maroon in color; terrestrial. Filaments long, contorted and tangled or rarely straight to flexuous for short distances, thickly interwoven, branching rarely, holding mostly a single trichome, rarely two, 2.4–3.5μ in diameter. Trichomes 1.7–2.4μ in diameter, often constricted slightly at the cross walls, often unconstricted and with inconspicuous cross walls. Sheaths faintly lamellate to
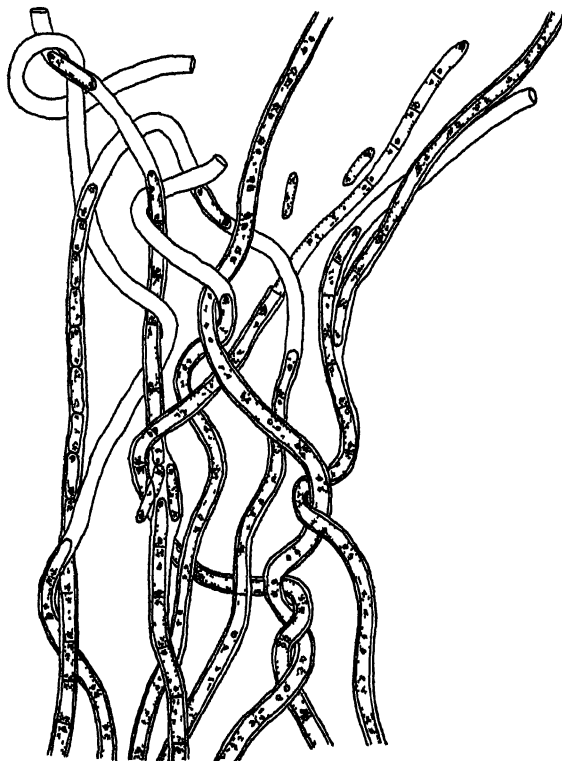
Fig. 72.—*Schizothrix thermophila,* group of filaments, some shedding unicellular hormogonia (×900).

homogeneous, firm, smooth, up to 0.6μ in thickness, pale reddish-brown, yellowish or pale orange, when young often hyaline. Cells 1.5–3.0 diameters in length, mostly with a few prominent granules often polar in position; end-cells rounded, unmodified. Hormogonia numerous, one-celled.

The pigmented sheaths and the felt-like strata place *S. thermophila* in the subgenus *Chromosiphon.* Its closest allies seem to be *S. Gomontii* Weber van Bosse and *S. fuscescens* Kützing. From the former it differs

in having longer cells, less lamellate and thinner sheaths, and an unelaborated stratum; from the latter, in its less frequent branching, its reddish sheaths and maroon stratum, and in having mostly single trichomes in the filaments. The unicellular hormogonia are unique.

Growing with *Scytonema caldarium terrestre* (of this paper), *Stigonema hormoides* (Kütz.) Born. et Flah. and *Albrightia tortuosa* (of this paper), this species is characteristic of the warm, wet edges and adjacent flats of the Hot Lake and Firehole Lake region in the Lower Geyser Basin. The dark maroon hue of the alga is a prominent feature in the entire region. There have been, for the past several years, square yards of almost pure *S. thermophila* in the flats at the west end of Firehole Lake. In spite of its local abundance it has not been found elsewhere. It seems remarkable that so abundant a species, growing in a site visited by almost all who come to the Park, should have remained unnoticed. It has been collected around the Black Warrior Springs, Hot Lake, Leather Pool, and Firehole Lake. Its temperature range was from 26° to 43° C., its acidity range from pH. 8.0 to 8.9. The type (no. 401) was collected between Young Hopeful Geyser and Firehole Lake, at 31° C.

DASYGLOEA Thwaites

Trichomes comparatively few in a broad ample sheath, widely separated from each other. Sheaths hyaline to pale yellowish, lamellate or not, firm or somewhat slimy. Filaments branched, often tangled, united into a slimy or gelatinous stratum.

Type species: *Dasygloea amorpha* Thwaites.

The genus, until now, has been composed of a single species. This one, *D. amorpha*, is known in the United States only from Onoko, Pennsylvania (Wolle, 1877). There are no previous records of *Dasygloea* from thermal sources.

A single Yellowstone species.

1. Dasygloea yellowstonensis, sp. nov.

Stratum thin, grayish green, gelatinous, fibrous, poorly developed; often mixed with other algae. Filaments twisted and entangled, uneven, gradually tapering at the apices, sparsely to frequently branching, up to 50μ in diameter and 1 mm. or more in length. Sheaths hyaline or pale yellow-brown within and hyaline without, lamellate, wide, uneven outside, and often dirt-covered. Trichomes 1 to 8, mostly 3 to 5, in a filament, 1.8–2.1μ in diameter, not constricted at the cross walls. Cells long-cylindrical, 2 to 6 diameters in length; with densely and coarsely granular contents, blue-green; cross walls often inconspicuous. End-cell rounded, neither tapering nor capitate.

D. yellowstonensis differs from *D. amorpha* in having more slender trichomes, unconstricted trichomes, proportionally longer cells, and simple tapering filament ends. The species are similar in the general nature of the sheath, the widely separated trichomes, and the tangled plant masses.

D. yellowstonensis has been noted in the Yellowstone only in the Meadow Springs, on moist soil and rock in the vapor and steam from
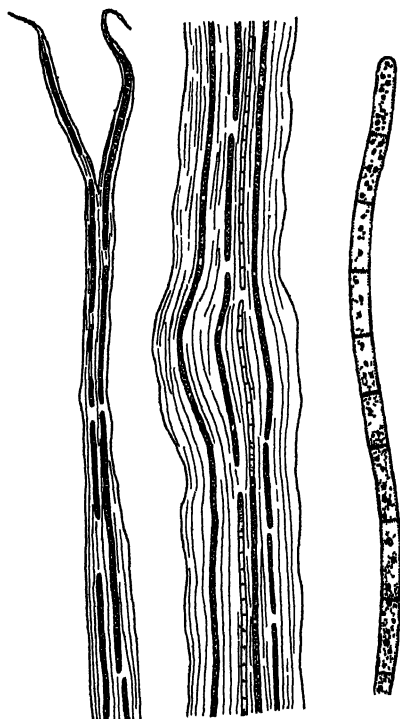
Fig. 73.—*Dasygloea yellowstonensis*, left, tip of filament (×330); center, middle portion of mature filament (×330); right, trichome (×1250).

hot springs. The type (no. 177) was growing at 38° C. The species is most frequently found at about 32° C., and has been noted at from 26° C. to 44° C.

MICROCOLEUS Desmazieres

Catal. pl. belg., p. 7, 1823.

Filaments often forming slimy indefinite strata. Filaments unbranched or sparingly branched, mostly cylindrical for the greater part and mostly tapering

toward the apices. Sheaths mostly colorless, homogeneous, soft, and mostly slimy, often thick, often difficultly visible, often confluent at maturity. Trichomes many to very many in each sheath, closely packed, and often entwined and rope-like. Trichome ends straight, often tapering and narrowed. End-cells mostly conical, sometimes capitate.

The species of *Microcoleus* inhabit salt and brackish water, salt marshes, etc., standing and flowing fresh water, moist rocks, tree trunks, soil, etc., and thermal springs. Of the thermal types *M. sociatus* W. & G. S. West (incl. *M. thermalis* Vouk) has been found in warm springs in France, Hungary, Croatia, Angola, and Turkestan; *M. Steenstrupii* Boye Pet. in hot springs in Iceland; and *M. paludosus* (Kütz.) Gom. in a warm spring near Puna, Hawaii, at 31° C. (Tilden).

In the Yellowstone the genus is of little importance.

A single Yellowstone species.

1. MICROCOLEUS STEENSTRUPII Boye Petersen

Freshw. Cyan. Iceland, p. 292, 1923.

Filaments 30–65μ in diameter, unbranched or occasionally branched. Sheaths distinct, colorless, scarcely lamellate, up to 20μ in thickness, holding numerous trichomes. Trichomes often corded and twisted, 3–5μ in diameter, feebly or not at all constricted at the cross walls. End-cells long-conical, neither capitate nor calyptrate, up to 13μ in length.

Up to the present there has been the single record of Boye Petersen from Iceland for the species.

In the Yellowstone it is occasional in the basic waters of the Geyser Basins. It has been noted in Jelly Spring in the Lower Geyser Basin (34.6° C.) and in Chromatic Spring in the Upper Geyser Basin (28.0° C., pH. 8.1.).

UPPER TEMPERATURE LIMITS FOR LIFE

The living organisms fall into two distinct groups that differ sharply in their potential tolerance to elevated temperatures. The nucleated plants and all animals exhibit, at most, an ability to endure heat up to 52° C. Brues (1924, 1928, 1932) has presented abundant data showing that 50–51° C. is the upper limit for animals. There are no reliable records for the occurrence of plants with nucleated cells at temperatures in excess of approximately the same degree. In opposition, Myxophyceae and Bacteria in many cases grow normally at several degrees in excess of this.

Maximum Temperature Records*

For Certain Groups of Organisms

Group	Highest Temperature Noted in Present Study—Former Studies	Highest known Temperature.
Myxophyceae	85.2° C. ...85.0° C. (West)	85.2° C.
Chroococcales	84.0° C.	84.0° C.
Chamaesiphonales	80.0° C.	80.0° C.
Oscillatoriales	85.2° C. ...85.0° C. (West)	85.2° C.
Bacteria	88.0° C. ...89.0° C. (Setchell)	89.0° C.
Chrysophyceae	40.2° C.	40.2° C.
Cryptophyceae	39.9° C.	39.9° C.
Bacillariae	50.7° C.	50.7° C.
Heterokontae	32.5° C.	32.5° C.
Chlorophyceae	50.5° C. ...48.0° C. (DeLaures)	50.5° C.
Isokontae	48.5° C. ...48.0° C. (DeLaures)	48.5° C.
Stephanokontae	27.6° C.	27.6° C.
Conjugatae	50.5° C.	50.5° C.
Phycomycetes	37.2° C.	37.2° C.
Charophyceae	38.1° C.	38.1° C.
Bryophyta	43.0° C.	43.0° C.
Pteridophyta	26.0° C.	26.0° C.
Gymnospermae	46.4° C.	46.4° C.
Angiospermae	49.8° C.	49.8° C.
Protozoa	42.8° C. ...52.0° C.(?) (Issel)	52.0° C.(?)
Mastigophora	36.0° C. ...37.0° C. (Cleveland)	37.0° C.
Sarcodina	42.8° C. ...52.0° C.(?) (Issel)	52.0° C.(?)
Infusoria	39.4° C. ...51.0° C. (Issel)	51.0° C.
Nemathelminthes	42.0° C. ...40.0° C. (Issel)	42.0° C.
Rotifera	33.0° C. ...45.0° C. (Hoeppli, etc.).	45.0° C.
Annelida	40.0° C.	40.0° C.
Mollusca	41.0° C. ...52.0° C.(?) (Studer)	52.0° C.(?)
Arthropoda	50.0° C. ...51.0° C. (Wood)	51.0° C.
Arachnida	48.3° C. ...51.0° C. (Wood)	51.0° C.
Crustacea	46.0° C. ...50.5° C. (Monterz)	50.5° C.
Insecta	50.0° C. ...50.0° C. (Brues)	50.0° C.

An upper temperature limit for life has never been satisfactorily established. The many records in part apply to the ability for continued or satisfactory growth, others were secured by experimental exposure of various organisms to elevated temperatures for varying periods of time. In some cases dormant structures (spores, cysts, tubers, etc.) have been employed. The majority of studies have dealt with few or non-representative species. The obvious impossibility of certain records (e.g., Sonnerat,

* Many records have been disregarded in the compilation of this table. Several of those omitted are highly improbable, and others do not add to the data presented.

1776, fish living in water at 86° C.) has led to notable skepticism toward the growth of organisms at temperatures quite favorable to certain species. The reported tolerance of seeds of certain Angiosperms, and of spores of various fungi and algae to temperatures above 51° C. is in need of confirmation. In the table above the applicable data on the upper temperature for growth of organisms of certain groups are summarized.

The cardinal temperatures (the optimum or most favorable for growth, the minimum or lowest at which growth will occur, and the maximum or highest which will permit growth) are known to vary with changes in the chemical environment. It is advisable to restrict their application to behavior under the most favorable conditions that can be obtained for the organism. Similarly the growth temperature range includes the greatest range in which the plant or animal can grow when the environment is satisfactory. In general the optima are easily determinable; the minima and maxima difficult because of the truncation of temperature range by variations in acidity, concentration and availability of solutes, light intensity, etc. The so-called thermal death point has been shown to be nonexistant (Bigelow and Esty, 1920, Bigelow, 1921), and thermal killing to be a function of temperature and length of exposure, subject to modification by variations in the environment. By shortening the exposure, higher temperatures may be survived. Thus, spores of *Bacillus subtilis* are killed by 80° C. or less if the exposure is prolonged to above three days, and are not destroyed at 130° C. in less than two minutes (Meyer, 1906). Similar effects have been obtained by numerous other workers. It is probable that with indefinite exposures, thermal death will occur at or near the maximum temperature (for growth).

The Myxophyceae and Bacteria are known to grow at temperatures in excess of those withstood by other organisms. Setchell (1903), in the Yellowstone, found blue-green algae growing at 75–77° C. and bacteria at 89° C. In Tibet, Hooker (1851) found *Leptothrix* (=*Phormidium*) at 75.5° C. Strachey (teste DeVarigny, 1893) observed algae in the same region at 78.8° C. West (1902) gave 85° C. as the upper limit for algal growth in the geysers and hot springs of Iceland. Schmid and Weis (1902) reported live algae in water at above 90° C. (not necessarily growing at this temperature!). Brewer (1866) claimed to have found algae at 91.5° C. in springs in California. Miquel (1888) isolated and studied the first well-known thermal bacterium, *Bacillus thermophilus;* it grew at temperatures up to 72° C. Other investigators have found bacteria that grew, in culture, at temperatures of 70–80° C. Setchell's record of 89° C. is probably the highest legitimate observation for the growth of

bacteria. In this study the maximum temperature of 85.2° C. has been noted for the blue-green algae. *Phormidium bijahensis* and *Oscillatoria filiformis* have been found growing in water that for several weeks before the final observation did not drop below that temperature. Unidentified bacteria were found, in a similarly checked situation, at 88° C. These temperatures are significantly close to West's figure of 85° C. and Setchell's of 89° C. for the same groups of plants. The maxima of 85.2° C. and 89.0° C. may be tentatively set for the Myxophyceae and Bacteria.

The temperature limits of the other plant groups are in no case in excess of 51.0° C. Mrs. Brues (in Brues, 1932) noted *Distichlis spicata* with roots in soil at 52.5° C. The author has noted an unidentified grass (sterile) rooted in friable sinter at almost the same temperature. Upon cytological examination the roots were found to be stunted and not undergoing cell division. Unquestionably the plant was unable to withstand that temperature, but with the support of the above-ground parts functioning under non-thermal conditions, the plant as a whole remained alive. Diatoms have been credited to water well above 50-51° C. The probability of these records is extremely low, since the majority of workers clean and mount their material before study, and have no method of determining which species were living when collected. Frustules of dead diatoms are regularly found in certain hot springs at all temperatures, and their presence is of no ecological interest. In Imperial Geyser the author has noted abundant and perfect diatom frustules in water at 89° C.; the geyser crater was recently blown through an old sinter-diatom deposit, and the specimens found in the spring are much older than the geyser. This spring came into being in 1928, and the diatoms had been dead at least 80 years. Thermal observations on this group must be made with living or well-preserved material.

The possibility of error in temperature determination is great, due to fluctuations and local variations. Many springs have decided cycles of activity and records for organisms from these springs must be made at the time of lowest temperature. Infrequently the activity of a spring will be accelerated and the temperature rise a few or many degrees. In such a spring old algal masses may remain in identifiable condition for several days and lead to erroneous temperature records. Water from large geysers may be blown over and heat strata of algae many degrees above their limit for growth. The temperature of water in hot springs may be several degrees higher than in the algal strata that are washed by the water. Consequently there are numerous improbable records in the literature, and considerable care must be used in considering them.

NATURE OF THERMAL SUSCEPTIBILITY AND TOLERANCE

To account for the notable difference in tolerance of the groups of organisms several theories have been advanced.

Mereschkowsky (1910, 1920) assumed the existence of two types of protoplasm, the one type (mycoplasma), with special properties including heat tolerance, present in the bacteria and blue-green algae, the second type (amoebaplasma) (associated with symbiotic units of the former as nuclei, plastids, etc.,) comprising the groundwork of the protoplasm of the other organisms. His complex symbiosis theory is not at all involved in the problem of thermal tolerance. The distinction of two types of protoplasm has merit and is emphasized by the many peculiar features of the Schizophytes (lack of nuclei, plastids, kinetic apparatus, golgi apparatus, chondriosomes, absence of sexuality, tolerance to high temperatures, to certain toxins, etc.), but it should be noted that many Schizophytes are not at all tolerant toward elevated temperatures.

Brues (1928) suggested that destruction of the chondriosomes (not known in Schizophytes) might account for the inability of the higher organisms to survive elevated temperatures. He states that the visible destruction of these bodies takes place at 48–50° C., approximately the upper limit for life of the groups that possess them. There is, at present, no direct evidence to support the view that chondriosomes are essential to life. Organisms of certain groups are killed by heat much below that said to destroy these bodies. Thus marine Coelenterata (Mayer, 1917) are unable to endure temperatures above 38.2° C., Echinodermata are tolerant at most of water at 30–32° C. (Jacobs, 1919), and the brown alga *Desmarestia viridis* is killed at 30° C. At such low but lethal temperatures the chondriosomes have not been shown to be injured, and apparently are not the critically susceptible structures. In cells killed by various agencies (poisons, etc.,) the chondriosomes are often the first cell structures to show visible disintegration, and it is probable that their deterioration is a result rather than a cause of death.

Several workers have suggested that the thermal organisms are a vestige of a primordial thermal flora and fauna. This view is so old that it is impossible to credit it to any single person. Schnetzler (1889) thought the thermal Oscillatoriae (incl. *Phormidium*) and certain thermal diatoms had such an origin. Setchell (1903) considered this theory in dealing with the Yellowstone organisms. Recently Vouk (1923) discussed it at some length. This theory may fall in line with Mereschkowsky's theory of the two types of protoplasm, the one an archaic type found in the relicts of the primordial life, the other a modern type found in recent types of

life. Brues (1928) has satisfactorily shown that the thermal animals are invaders of warm waters rather than types that have always been there, and that they are chiefly members of specialized groups with no primitive characters. His conclusions apply as well to the nucleated plants, and there are left to be considered in this theory only the Schizophytes. Objection may be raised to the existence of former thermal conditions on the earth, especially since the partial discard by geologists of the once popular nebular hypothesis and the substitution of the planetesimal hypothesis. This possible objection is feeble. There are geological remains of hot springs as far back as the early Paleozoic, and probable hot spring formations in the Proterozoic strata. Volcanic action (at present regularly followed by the production of hot springs) certainly has occurred throughout the earth's history (at least from Archean to present). It is not necessary to postulate general thermal conditions or even larger numbers of thermal springs than are now in existence, to permit the development of an early thermal flora and its continuity to the present.

Among the present-day Schizophytes, just as with nucleated organisms, there are distinct specific thermal limits. Some blue-green algae have a very low temperature range; this is paralleled by the psychrophilic (cryophilic) bacteria and by certain nucleated plants and animals. Others have their ranges covering a moderate temperature. The Schizophytes are peculiar, not in lacking thermal specificity, not in including only forms able to live at high temperatures, but in including thermophilic species whose ranges extend above 51° C. It is suggested that the thermal blue-green algae and bacteria have given rise, at various times, to mesophilic forms. These in turn have given rise to other mesophilic types, and in certain cases to the psychrophilic and to the secondarily thermophilic forms. The origin of all the non-thermal species directly from thermal ones is not probable and is certainly not indicated by the available evidence.

The differentiation of organisms into (artificial) groups on the basis of optimum temperatures is flexible. Many authors have followed the system used above: psychrophilic organisms with optima below 20° C., mesophilic with optima between 20° C. and 45° C., and thermophilic with optima above 45° C. With these definitions there are probably no truly thermophilic nucleated plants or animals. The numerous special terms variously employed to designate certain types of temperature relationships are in need of standardization or definition when used.

The essential problem of thermal tolerance and susceptibility is the finding of factors or processes that determine specific temperature

ranges, and secondarily the determination of the cause of thermal killing. The Schizophytes are more adaptable in the first, more resistant toward the second.

Differential temperature coefficients for the several processes in metabolism may account for the specific temperature ranges. Zinsser (1931) suggested that the temperature coefficient of the catabolic reactions is greater than for the anabolic processes. With an increase in temperature there results an increase in rate of all chemical and physical reactions, producing greater efficiency up to an optimum for growth. Above this point further increase in temperature would accelerate the catabolic processes to such an extent that the anabolic processes would be more nearly neutralized and a metabolic balance in the cells could be maintained only with a diminution in growth. At a rather definite temperature (the maximum) a final and critical balance would be reached at which growth would be stopped. At this point constructive and destructive metabolism would exactly balance. If the temperature was raised further, catabolism would exceed anabolism and death would eventually ensue. This theory is in harmony with the known behavior toward elevated temperatures. Length of exposure is definitely linked with killing effect. This implies a progressive process rather than an immediate destruction. Thermal acclimatization to a limited extent has been produced in numerous organisms. This is possible only if thermal adjustment is due to a function or process that is readily changed by the protoplasm of the cells. Following death by metabolic unbalance, visible disintegration (of chondriosomes, etc.,) or coagulation could proceed variously. Pütter (1914) held a view similar to that of Zinsser. He postulated a constant value of Q_{10} for a "basic reaction" and a higher value for a "Gegenreaction". With an increase in temperature the reverse reaction would gradually neutralize the constructive processes.

The endurance of especially high temperatures by bacterial spores has been tentatively explained by the assumption that "since heat killing is due to protoplasmic coagulation, increase in the concentration of the protoplasm (as in spores, cysts, etc.,) would raise the coagulation point". This assumption (true in respect to concentration effect on coagulation of certain proteins) is not based on necessarily applicable evidence. The bulk of work on protein coagulation has dealt with reserve proteins (as in seeds, egg albumen, etc.,), and may not apply to protoplasm. The proteins of heat-resisting spores are unknown. In resting structures vital processes are carried on at a reduced rate. This reduction must be due either to lower concentration of the catalysts effecting metabolism, or to

the lowered supply of materials for the reactions. In either case the acceleration by a temperature rise to above the maximum would cause death less promptly due to the inherently slower rates of the processes that speeded up to the potentially lethal point. Up to the present no spores have been shown to be immune to killing by temperatures fatal to active cells of the same species, when the exposure is prolonged. Heat tolerance of spores exists for definitely limited durations only.

THERMAL DISTRIBUTION OF THE YELLOWSTONE MYXOPHYCEAE

The vigor of growth and abundance of Myxophyceae in thermal waters are apparently greater than in cooler habitats. Strata of the various blue-green algae solidly cover the bottoms and sides of all physically satisfactory springs and overflows at temperatures up to cir. 65° C. Above that temperature the abundance gradually decreases. The Myxophyceae are much more abundant in thermal than non-thermal sites in the Yellowstone. Strata of *Phormidium* ten centimeters thick occur in some springs. The great abundance results in sharp competition, and many species live as epiphytes.

THERMAL DISTRIBUTION OF YELLOWSTONE MYXOPHYCEAE

Temperature	Species & Varieties	Number of Genera	Families	Orders
10–15° C	42	15	6	3
15–20° C	54	21	7	3
20–25° C	76	27	8	3
25–30° C	86	34	11	3
30–35° C	90	35	11	3
35–40° C	86	34	13	3
40–45° C	76	30	13	
45–50° C	60	20	12	
50–55° C	50	17	9	
55–60° C	43	14	9	3
60–65° C	29	10	7	3
65–70° C	18	6	5	3
70–75° C	9	5	4	3
75–80° C	6	4	3	3
80–85° C	6	4	3	3
85–90° C	2	2	1	1
90–95° C	0	0	0	0

The greatest number of species was noted at cir. 35° C. Possibly some significance may be drawn from the close approximation of this to the temperature of the many homoeothermal animals. Several species exhib-

ited a wide temperature range (up to 46° C.) but the majority were important through ranges of less than 25° C.

Reaction of the water (pH.) exerts a marked effect on distribution, and apparently the greatest abundance of Myxophyceae occurs at cir. pH. 8.0. The total range noted in the springs with algal growth was pH. 2.65–9.40. Few species existed through a range of more than 3.00 units, and the majority were restricted to a range of 2.00 units or less.

REACTION DISTRIBUTION OF YELLOWSTONE MYXOPHYCEAE

Acidity	Species & Varieties	Number of Genera	Families	Orders
pH. 2.6–3.0	1	1	1	1
pH. 3.0–3.4	1	1	1	1
pH. 3.4–3.8	1	1	1	1
pH. 3.8–4.2	1	1	1	1
pH. 4.2–4.6	2	2	2	2
pH. 4.6–5.0	4	4	4	3
pH. 5.0–5.4	11	8	6	3
pH. 5.4–5.8	14	9	6	3
pH. 5.8–6.2	24	12	6	3
pH. 6.2–6.6	40	18	9	3
pH. 6.6–7.0	53	21	11	3
pH. 7.0–7.4	68	23	11	3
pH. 7.4–7.8	72	24	11	3
pH. 7.8–8.2	92	31	11	3
pH. 8.2–8.6	84	29	10	3
pH. 8.6–9.0	58	21	9	3
pH. 9.0–9.4	26	12	7	3

The thermal waters of the Yellowstone are deficient in combined nitrogen, and all thermal springs are low in dissolved oxygen. Other necessary substances are generally present in satisfactory amounts. The nitrogen deficiency seems to have no marked effect on growth or normality of the blue-green algae. The oxygen shortage seems to be of little consequence, and apparently considerable oxygen is liberated in photosynthesis.

With the exception of a very few springs (Chocolate Pots, Soda Spring, etc.,) distribution seems to depend chiefly on temperature, pH. of water, supply of water, and amount of light. Within the Park little evidence of isolation is shown by the flora of the several springs.

ORIGIN AND RELATIONSHIPS OF THE YELLOWSTONE THERMAL FLORA

The Yellowstone thermal algae may be conveniently divided into five rather definite groups on the basis of their ecological and phyletic relationships.

I. Tropical species occurring in thermal sites of approximately the same nature as those favored in the tropics. A few species as *Plectonema Dangeardii* Frémy, *Oscillatoria Lemmermannii* Wolosz., and *Rivularia globiceps* G. S. West are known only from the tropics and from slightly warm thermal waters.

II. Local species (incl. cosmopolitan forms) of cool waters occurring in the cooler thermal waters. Many local species invade the thermal springs, and are often important up to 30° C. They rarely occur above 40° C. and become more abundant as the waters cool to temperatures comparable with those of meteoric waters. Such important species as *Gloeocapsa arenaria* (Hass.) Rab., *G. rupestris* Kütz., *G. stegophila* (Itz.) Rab., *Aphanothece saxicola* Naeg., *Chamaesiphon incrustans* Grun., *Stigonema hormoides* (Kütz.) Born. & Flah., *Calothrix fusca* (Kütz.) Born. et Flah., *Tolypothrix distorta* Kütz., *Nostoc parmelioides* Kütz., and many of the plants of groups other that the Myxophyceae are of this type. Many animals of thermal waters are of the same nature.

III. Facultative species of wide geographical range and great tolerance to diverse and variable conditions. Many of the blue-green algae occur in several of the more difficult or unusual habitats: warm water, brackish water, sulphide springs, sulphur springs, iron springs, mineral springs, polluted water, damp mud, and caves. Among the Yellowstone species of this group are *Spirulina maior* Kütz., *Oscillatoria chalybea* Mert., *O. amphibia* Ag., *O. terebriformis* (Ag.) Gom., *O. splendida* Grev., *O. amoena* (Kütz.) Gom., *O. formosa* Bory, and *Phormidium tenue* (Menegh.) Gom. In general they are restricted to water below 51° C., and include both transitional and low thermal forms. According to the data of Brues (1928, 1932) many animals fall into this group, and apparently several of the nucleated plants are comparable in their relationships.

IV. Varieties and species closely related to non-thermal forms, but occurring chiefly or exclusively in thermal waters. Such forms as *Chroococcus minutus* var. *fuscus* (of this paper), *Synechococcus elongatus* var. *amphigranulatus* (of this paper), *Microchaete bulbosa* (of this paper), *Spirulina labyrinthiformis* Menegh., and *Oscillatoria Boryana* (Ag.) Bory represent this group. The thermal diatom, *Denticula thermalis* Kütz., certain Conjugatae, and some thermal animals are to be placed here. Low and moderately typical thermal species that may (with the Myxophyceae) extend into water as hot as 65° C. make up this group.

V. Truly thermal species most closely related to other thermal organisms and in many cases of groups restricted to thermal waters. The many

high thermal and the several thermal limital species of Myxophyceae (and Bacteria) are grouped into this alliance. Several low thermal and transitional forms are allied with them and may be considered as derivatives that in cases are adjusted to lower temperature ranges. No nucleated organisms are of this type. Such genera as *Thalpophila, Colteronema, Albrightia, Pluto*, and *Bacillosiphon*, such species groups as the extremely minute species of *Phormidium* and the elongate species of *Synechococcus* make up this collection of typical thermophilic organisms.

The truly thermal species give no evidence of having been derived from non-thermal sources. It seems probable that they represent stocks that have always lived in water of an elevated temperature. Quite possibly the Myxophyceae, as a class, originated in hot water, and the numerous modern cool water species have been derived from thermal ancestry. It is certain that the Myxophyceae and Bacteria occupy a position not to be assumed by the incidental and aberrant thermal representatives of the higher organisms. All of the orders, most of the families, and the majority of the important genera of the blue-green algae include thermal species. The morphologically and nutritionally most primitive organisms include the Myxophyceae, and their notable incidence in thermal habitats suggests the probability of the origin of living organisms in the thermal waters.

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I

YELLOWSTONE THERMAL MYXOPHYCEAE

New names and final members of new combinations are in **bold face type**. Where several page numbers follow a name, the one printed in **bold face type** is that on which the technical description of the plant occurs. Synonyms are in *italic type*.